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THE ORIGIN OF TOXIC AMMONIA IN GERMINATING GARDEN BEET SEED

By S. REHM
Division of Horticulture, Pretoria

THE problem of germination inhibitors is of the greatest practical importance in the technique of seed testing. In soil, these substances generally have no influence on the germination because they are made harmless by absorption, whereas, in the germination test, the seed lies on filter paper or cotton which have a much lower absorption capacity than soil. Consequently, in the germination test, the presence or the accumulation of toxic substances may result in a lower germination percentage than the same seed would show under natural conditions in soil.

With beet seed, the official method (Eggebrecht, 1949, Franck, 1949) prescribes that the seed be washed in running water to remove the inhibiting substances before the seed is put in the dishes for germination. Nevertheless there still remains a toxic principle in the seed balls ; after a few days the rootlets of the seedlings become black and die, and the germination is generally less than in soil. Stout and Tolman (1941) have shown that this is due to ammonia which is set free from amides and other nitrogenous compounds by enzymes. There are apparently two entirely different toxic principles in beet seed :

(1) " Primary " inhibitors which are present in the dry seed and are removed by washing, such as inorganic salts (Duym *et al.*, 1947) and organic inhibitors (Fröschel, 1940, 1945 ; de Kock and Hunter, 1950).
(2) " Secondary " inhibitors which are not present in the beginning but develop during germination.

The present paper is concerned only with the second group and the results of Stout and Tolman (1941) are confirmed, viz. that it is free ammonia which causes the inhibition of germination and the blackening of the rootlets in this stage. Entirely different conclusions, however, are reached about the origin of the ammonia.

MATERIAL AND METHODS.

The beet variety used was Detroit and the seed was harvested on the 29th to 30th December, 1947, from an experimental plot at Fonteinplaas Experiment Station, Oudtshoorn. The experiments here described were carried out from June to November, 1949. For germination, 50 seeds were placed on filter paper wetted with 5 ml. distilled water and in Petri dishes of 9 cm. diameter. The dishes were kept in a dark place at room temperature.

Nitrate nitrogen was determined after reduction with Devardas alloy in alkaline solution ; nitrite nitrogen with the Griess reagent and a photoelectric colorimeter ; free ammonia by distillation in vacuo at 30° C. ; ammonium nitrogen by vacuum distillation after addition of MgO ; amide nitrogen after hydrolysis by boiling the solution for 2 hours in 10 per cent. H_2SO_4. The protein N was precipitated by sodium tungstate at pH 1. For the determination of the pH, a Beckman pH-meter with glass electrode was used.

RESULTS.

(1) *Chemical analyses.*

In previous experiments, A. J. van der Merwe (Division of Horticulture, Pretoria, unpublished data) showed that in germinating garden beet seed a certain amount of nitrite can be found. As this did not agree with the results of Stout and Tolman, it seemed desirable to reinvestigate the whole problem of changes in nitrogen compounds during germination.

Table I shows the nitrogen fractions of untreated seed as well as of seed washed for 2 hours in running tap water.

TABLE I.

Nitrogen fractions (mg.) of 1 gr. dry beet seed.

	Unwashed seed	Washed seed
	mg.	mg.
Protein	17·7	17·2
Total soluble N ..	3·91	2·01
Free ammonia N ..	—	—
Ammonium N ..	0·40	0·20
Amide N	0·17	0·10
Nitrate N	1·92	0·55
Nitrite N	—	—

The high nitrate content of the beet seed is the most remarkable feature of these analyses. The material consisted of sixty samples which had received various treatments, i.e. normal and double irrigation, different fertilizer applications and various methods of harvesting. All the seed samples contained nitrate, varying from 0·52 mg. to 2·25 mg. nitrate nitrogen per gram dry weight. The external factors influenced considerably the amount of nitrate present in the seed balls. It seems that nitrate may occur generally in beet seed, for Gillis (1940) found that water extracts of European sugar-beet seed contained a rather high amount of nitrate. The subject of nitrate content is discussed later in the present paper (p. 10), in relation to the work of Stout and Tolman (1941).

The washing removed approximately half the soluble nitrogen and nearly three-quarters of the nitrate. The nitrate cannot be extracted completely by washing because part of it is contained in the hard pericarp. Table II gives the nitrate content of the various parts of the unwashed seed balls after separation by hand.

TABLE II.

Nitrate N (mg.) per 1 gr. dry matter of the separated parts of unwashed beet seed balls.

Seed with testa	0·21 mg.
Hard pericarp	2·70 mg.
Dry perianth	4·40 mg.

It is known that the bacteria which develop on germinating seeds are able to reduce nitrate to nitrite and ammonia (Jorissen, 1885, Laurent, 1886, cited after Czapek, *Biochemie der Pflanzen*, Vol. II, p. 173). Gassner and Franke (1935) found that calcium nitrate added to germinating seed of *Lythrum salicaria* is quickly reduced and they ascribe this to the action of micro-organisms. On germinating beet seed there is a very rapid development of bacteria, and it seems probable that these bacteria are the cause of ammonia-formation by reduction of the nitrate originally present. Fig. 1 shows the changes in the nitrogen fractions during germination of unwashed beet seed. The nitrate is completely reduced in 14 days. Traces of nitrite nitrogen appear on the second day. From the beginning, the nitrite is further reduced to ammonia so that the total amount of nitrite never becomes very high. The amide nitrogen is low from the beginning and shows no significant changes during the fortnight. The production of ammonia may be even higher than the figure shows because there will occur a loss of ammonia in gas form ; the decrease in ammonia content after the eighth day can be explained accordingly. The total soluble nitrogen decreases from 3·3 to 1·8 mg. The protein nitrogen shows a small decrease only during the last four days of the experiment.

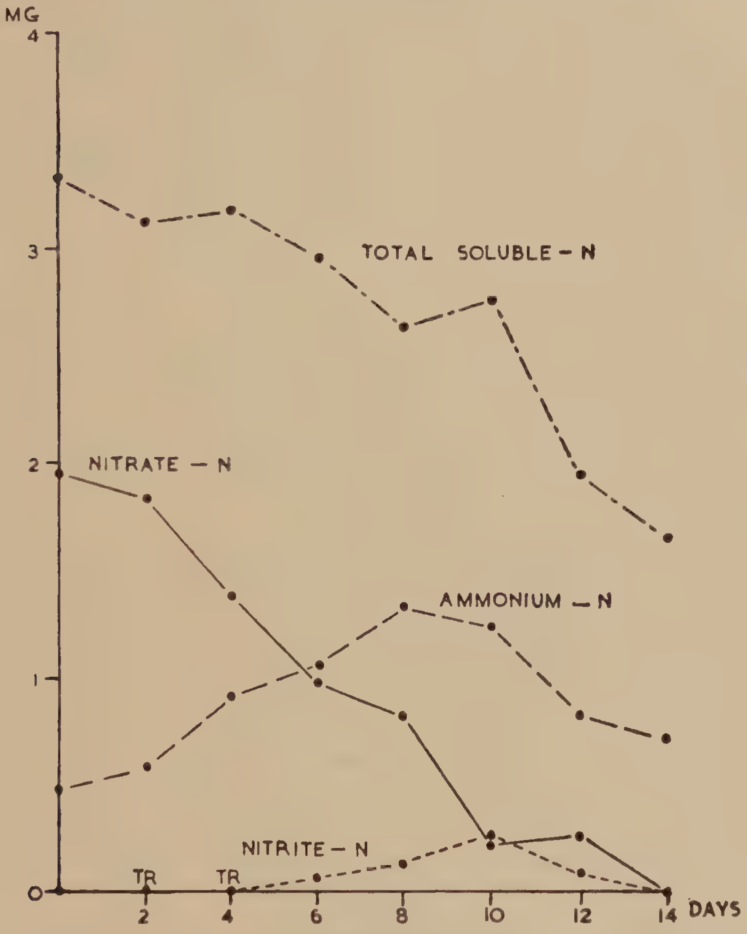

FIG. 1.

Changes in nitrogen fractions during germination of untreated beet seed (mg. N per 1 gr. dry seed).

Each value in the figure represents the average of three determinations. It is worth mentioning that the variation between the individual dishes is rather high. Table III gives the single values of ammonium and nitrite nitrogen for each of the three samples which were analysed on one day.'

TABLE III.

Single values of ammonium N and nitrite N during germination of beet seed. (*See Fig. 1.*) (*mg. N per gr. dry matter.*)

Days	Ammonium N			Nitrite N		
0	0·53	0·49	0·41	0·00	0·00	0·00
2	0·61	—	0·54	trace	trace	trace
4	0·80	0·92	0·98	trace	trace	trace
6	0·94	1·23	1·02	trace	0·16	0·01
8	1·36	1·35	1·24	0·18	0·12	0·10
10	1·30	1·19	1·20	0·47	0·00	0·34
12	1·07	0·87	0·49	0·18	0·07	0·00
14	—	0·70	0·70	0·00	0·00	0·00

To prove whether the assumption that the formation of ammonia is due to the action of bacteria is correct, several seed disinfectants were tried. No disinfectant was found which would completely prevent bacterial growth without damaging the germinability or the growth of the seedlings. The best results were obtained by

TABLE IV.

Beet seed washed for 2 hours in running tap water. Not disinfected. (*mg. N per 1 gr. dry seed.*)

Days	Protein	Total soluble N	Ammonium N	Amide N	Nitrate N	Nitrite N
0	17·2	2·07	0·20	0·10	0·55	0·00
3	17·2	2·07	0·60	0·09	0·22	0·00
5	17·3	1·85	0·60	0·11	0·11	trace
7	17·1	1·86	0·51	0·14	0·09	0·00
9	17·1	1·78	0·75	0·12	0·07	0·00
11	16·6	2·49	1·02	0·13	0·00	0·00

TABLE V.

Beet seed washed for 1 hour 40 minutes in running tap water and dipped for 20 minutes in 0·5 per cent. Aretan solution. (*mg. N per 1 gr. dry seed.*)

Days	Protein	Total soluble N	Ammonium N	Amide N	Nitrate N	Nitrite N
0	17·5	2·14	0·18	0·10	0·55	0·00
3	17·4	2·16	0·15	0·12	0·45	0·00
5	17·5	2·13	0·15	0·15	0·49	0·00
7	17·2	2·58	0·19	0·16	0·45	0·00
9	17·4	2·50	0·22	0·15	0·42	0·00
11	17·3	2·59	0·26	0·17	0·47	0·00

dipping the seed for 20 minutes in a 0·5 per cent. solution of Aretan. With this treatment some bacteria began to develop after several days, but never in such quantities as on seed not disinfected. The differences between disinfected seed and that not disinfected are, however, large enough to give a clear picture of the action of the bacteria.

The changes in the different nitrogen fractions during germination of washed seed not disinfected and of washed seed disinfected, are represented in Tables IV and V.

With the seed not disinfected there is a rapid decline in nitrate nitrogen during the first three days and a corresponding increase in ammonium nitrogen. During this period the other nitrogen fractions remain practically unchanged, so it may therefore be concluded that all the ammonia formed during the first days has its origin from the nitrate nitrogen in the seeds. Nitrite could be detected only in traces on the fifth day. Apparently all the nitrite was reduced to ammonia before it could

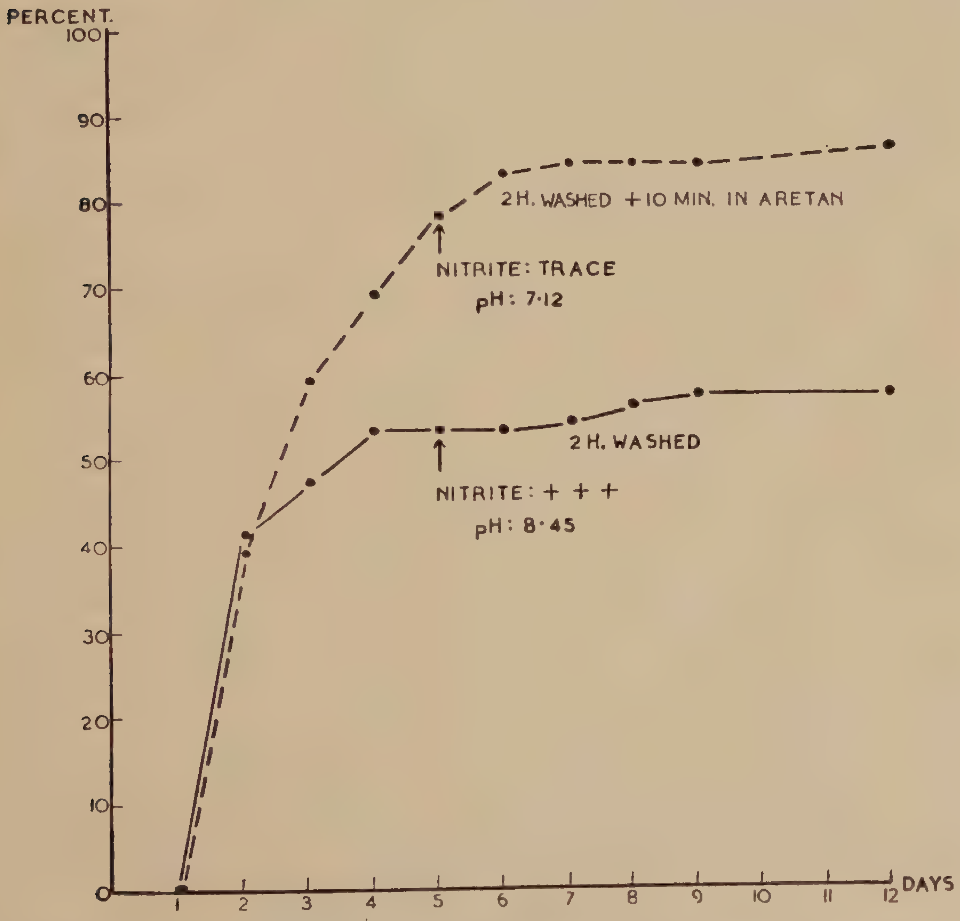

FIG. 2.

Germination of washed beet seed, not disinfected and disinfected in 0·5 per cent. Aretan solution.

accumulate in bigger quantities. Only at the end of the experiment a noticeable loss of protein nitrogen took place which led to a corresponding increase in soluble nitrogen and ammonium nitrogen.

With the disinfected seed, nitrate nitrogen and ammonium nitrogen remain almost constant. Germination and growth of the young seedlings are probably of more importance for the changes in the nitrogen compounds than is the very low bacterial growth. The increase in soluble nitrogen which occurs after the fifth day is probably due to the normal hydrolysis of proteins during germination.

(2) *Germination tests on filter paper.*

As Stout and Tolman have shown, ammonia is a very efficient inhibitor of germination. Therefore it must be expected that by disinfection, which suppresses the bacterial growth and thus the formation of the ammonia, we should get a better germination than with seed not disinfected. Fig. 2 gives a typical example. On the second day, when germination starts, it is as good in washed as in disinfected seed. But already, on the third day, the inhibiting effect of ammonia in the dishes with seed not disinfected is clearly visible and, from the fourth day onward, germination is practically suppressed, being only 57 per cent. after 12 days. In the dishes with disinfected seed, germination proceeds for several days and reaches 90 per cent. Nitrite content and pH values given in Fig. 2 indicate the nitrite reduction and the formation of germination-inhibiting ammonia.

The ammonia in the infected dishes is not only an inhibitor of germination but kills the young roots, which are very sensitive to ammonia in solution or as gas.

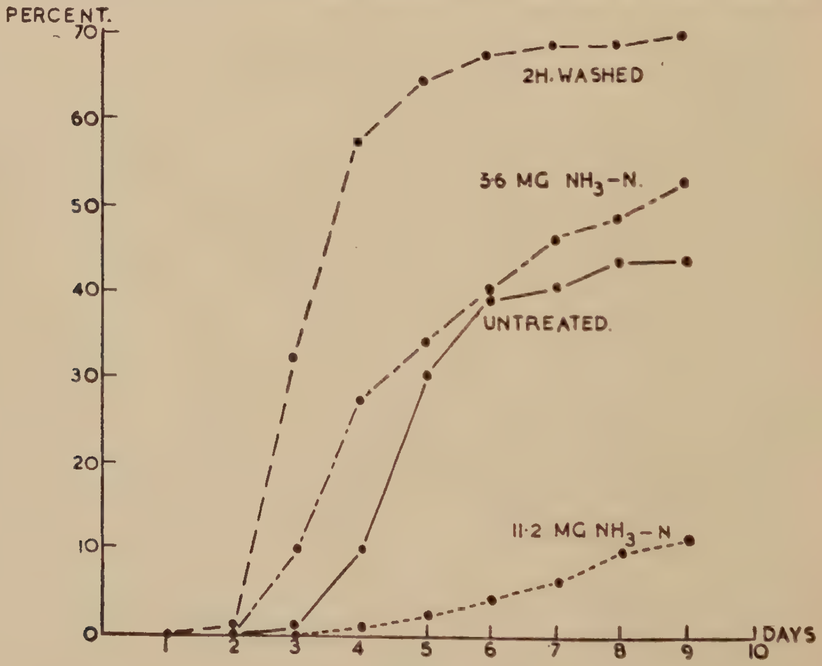

FIG. 3.

Germination of beet seed, washed and disinfected in 0·1 per cent. $HgCl_2$ solution; 5·6 mg. and 11·2 mg. ammonium N per dish added to the washed and disinfected seed.

The rootlets of the seedlings blacken and die within 24 hours if an appreciable amount of free ammonia is present. If the seed is disinfected, no ammonia develops and the seedlings grow in the dishes without any sign of damage. Fig. 3 illustrates an experiment in which ammonia was added to washed and disinfected seed. Ammonia diminishes the rate of germination and the germination percentage finally reached. The ammonia content was not kept at constant level, and some must have been lost by diffusion into the air. This probably explains the increasing germination in the ammonia dishes after the sixth day. The decisive factor for the germination is the concentration of free ammonia within the seed balls; this cannot be determined accurately, but the effect of externally added ammonia sufficiently illustrates the inhibiting action of free ammonia.

There also exists the possibility that the nitrite, which is sometimes formed in considerable amounts, may be poisonous for the seedlings, and be inhibiting to germination. In several experiments which were done in the dark and in diffuse daylight, it was shown that nitrite is not poisonous at the normal pH of 6·5 to 7·0 (or higher). Fig. 4 illustrates this type of test.

The nitrite content remained practically unchanged during this experiment.

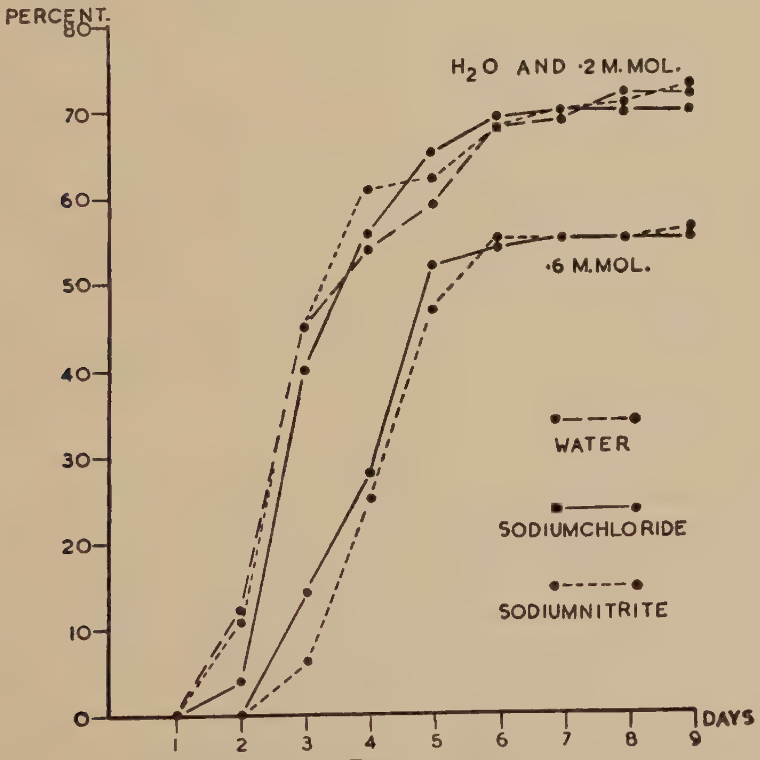

FIG. 4.

Germination of washed and disinfected beet seed.
Wetted with 5 ml. H_2O; 0·2 millimol (=11·7 mg.) NaCl in 5 ml. H_2O;
0·2 millimol (=13·8 mg.) $NaNO_2$ in 5 ml. H_2O;
0·6 millimol (=35·1 mg.) NaCl in 5 ml. H_2O;
0·6 millimol (=41·4 mg.) $NaNO_2$ in 5 ml. H_2O.

The germination in sodium nitrite solutions is the same as in equimolar sodium chloride solutions.

Incidentally, it may be mentioned that these experiments show that relatively weak solutions of inorganic salts have a strong inhibiting effect on the germination of beet seed, thus confirming the results of Duym *et al.* (1947).

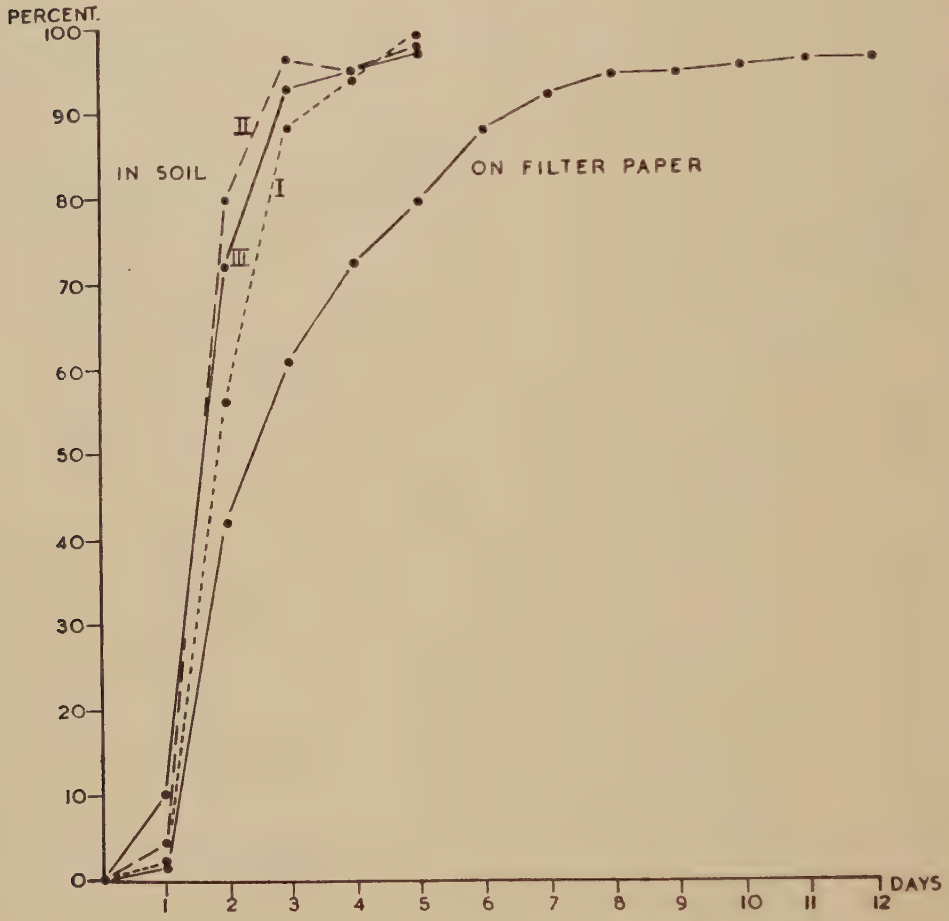

FIG. 5.

Germination of beet seed in soil : I = untreated seed ; II = seed 2 hours washed, not disinfected ; III = seed 1 hour 40 minutes washed, 20 minutes dipped in 0·5 per cent. Aretan solution. Germination on filter paper : seed 1 hour 40 minutes washed, 20 minutes dipped in 0·5 per cent. Aretan solution.

(3) *Germination in soil.*

For several reasons the question as to how the germination of beet seed in soil is influenced by bacteria, is of great interest.

Is ammonia formed in soil ? Has it the same inhibiting effect there on germination ? It depends upon the answer to these questions whether the disinfection of seed, which is necessary to get the maximum germination on filter paper, gives correct values in a germination test.

So far, we have made experiments with only one type of soil, a red sandy loam of pH 4·9. Petri dishes containing 100 gr. dry soil were sterilized at 150° C.; after cooling they were wetted with 25 ml. water, and 50 seeds put in the soil so that they were completely covered. The development of bacteria and the reduction of nitrate to ammonia *via* nitrite was the same as with seed on filter paper. The pH increased from 4·9 to 6·5 within six days. At pH 6·5 no free ammonia can exist; apparently the soil is able to absorb all the ammonia formed, with the consequence that there is no inhibition of the germination or poisonous effect on the rootlets.

Fig. 5 shows three remarkable differences between germination in soil and on filter paper. (1) Germination in soil is much quicker; 98 per cent. is the maximum germination of the material used; in soil, more than 90 per cent. has germinated after the fourth day, while, on filter paper, disinfected seed reaches this percentage only after seven days.

(2) The retardation due to the primary inhibitor(s) has nearly disappeared. Unwashed seed on filter paper germinates two to two-and-a-half days later than washed seed, while, in soil, the retardation is only about half a day.

(3) All treatments (unwashed, washed and disinfected) reach the maximum germination percentage. With regard to germinability, the washing and/or disinfecting of garden beet seed, prior to sowing, offers no advantage when the seed is sown in soil.

The comparison between germination in soil and on filter paper furnishes no objections to the use of disinfectants in the germination test, as the only object of this test is to establish the maximum germination percentage. Seed not disinfected and on filter paper never reached the maximum germination in our experiments.

It may be that under certain circumstances, in soils with a low absorption capacity, ammonia may accumulate to a poisonous concentration. But we can assume that, in light soils under normal field conditions, free ammonia will be washed out by surplus water or diffuse into the air.

Our investigations on the influence of bacteria on germination in soil are only preliminary and will be continued.

DISCUSSION.

The most striking fact established by our experiments is the great influence which bacteria have on the germination of beet seed. According to our experience, all the secondary effects inhibiting germination are due to the production of ammonia by bacteria. It is surprising to see how little attention is paid in the literature on the physiology of germination, to the possible interaction of bacteria. Only Gassner and Franke (1935) come to the conclusion that the changes in soluble nitrogen in the seed bed (filter paper) and the loss of nitrogen during germination must be ascribed to micro-organisms.

It is difficult or impossible—especially with the seed balls of beet—to work under strictly sterile conditions. If the disinfectants are applied in a concentration to prevent completely the development of bacteria, the germination power of the seeds inevitably is reduced. But by using weak solutions of mercuric chloride, formaldehyde or Aretan, the development of bacteria is suppressed, at least for the first four or five days, to such an extent that quite reliable conclusions may be drawn.

(1) Dipping for 10 minutes in 0·1 per cent. $HgCl_2$ solution and subsequent washing in running water gave good disinfection but a slight retardation of germination. Dipping in 0·5 per cent. or 1 per cent. formaldehyde and subsequent drying gave excellent disinfection and germination, but the disinfecting effect was lost after three to four days.

The best results for the germination test were obtained by dipping in 0·5 per cent. Aretan solution and subsequent drying without first washing off the adhering solution. The germination is not inhibited and the development of bacteria is delayed long enough to obtain maximum germination. But Aretan cannot be recommended for disinfection, if it is intended to raise a crop, because it produces an abnormal swelling of the hypocotyl and prevents the freeing of the cotyledons from the seed balls, so that the seedlings emerge slowly and irregularly from the soil.

(2) The second important result is that nitrate is the main source from which ammonia is formed on germinating beet seed. Bacteria of course are able to form ammonia from amides and amino acids, but the amide content of beet seed is very low and remains more or less constant during germination, so that this can add only a small fraction of the total ammonia which is formed. Proteolysis begins only after the fifth day or later (Tables IV and V), whereas ammonia is formed from the first or second day onward so that protein cannot be the source of the ammonia. Stout and Tolman in their work on production of ammonia in beet seed extract do not state from which nitrogenous compound of the original extract the ammonia actually was derived (p. 696 and Table 7 of their paper (1941)). Added amides they found were quickly hydrolysed, but the amide content of the original extract was low (Table 7), and was not significantly changed during germination. Unfortunately they did not determine the nitrate content of their material. In Table V, however, they report an experiment in which sodium nitrate was used as artificial source of nitrogen; the pH increased in this solution within 71 hours from 5·75 to 7·72 and ammonia was formed. We must conclude that in this experiment the same happened as in ours; that is to say their material was not sterile, bacteria developed and nitrate was reduced to ammonia. The change of pH and the formation of ammonia being as high with sodium nitrate as with most of the seed ball extracts in Table V of Stout and Tolman, it is very probable that their seed material also contained nitrate which was the source of the ammonia.

The growth of bacteria on germinating seed, and their metabolism, may be responsible for many of the controversies about the influence of external factors on germination. The composition and activity of the bacterial flora depend largely on temperature, humidity and light. We mentioned the great variation in the formation of ammonia and nitrite (Table III). As another example, we will refer to the pH found in single dishes of the same experiment: the pH may differ for more than one unit without any visible reason. The external conditions being identical in these experiments, the only explanation can be that the uncontrolled composition of the micro-flora has differed.

The germination of beet seed is especially sensitive to a surplus of water in the dishes. Probably this is due to the reaction of bacteria to changing water conditions. Bacterial growth is favoured by an excess of water, nitrate is more quickly reduced and more ammonia will remain dissolved. Table VI gives the pH values reached after eight days in a preliminary experiment on the influence of different quantities of water.

TABLE VI.

Beet seed not disinfected. pH after eight days.

5 ml. water per dish	7·51, 7·50, 7·60
10 ml. water per dish	8·49, 8·52, 8·01

All these points, i.e. the composition of the bacterial flora and the influence of the various external factors on the bacterial flora and the metabolism of the bacteria, need further investigation. Information gained as to this may be of practical value, not only in respect of the detrimental formation of ammonia but also in respect of a favourable influence which is indicated by some observations.

An experiment in which undisinfected seed was washed for different periods is shown in Fig. 6. The washed seed germinated at the beginning much more quickly than untreated seed but reached at the end a lower germination percentage. The only ready explanation of this phenomenon is that, on untreated seed, more bacteria and fungi develop, which produce germination-promoting substances or make inhibiting substances ineffective, for example by assimilating some of the ammonia or by excretion of acids which neutralize the ammonia. Investigations on this subject will be continued.

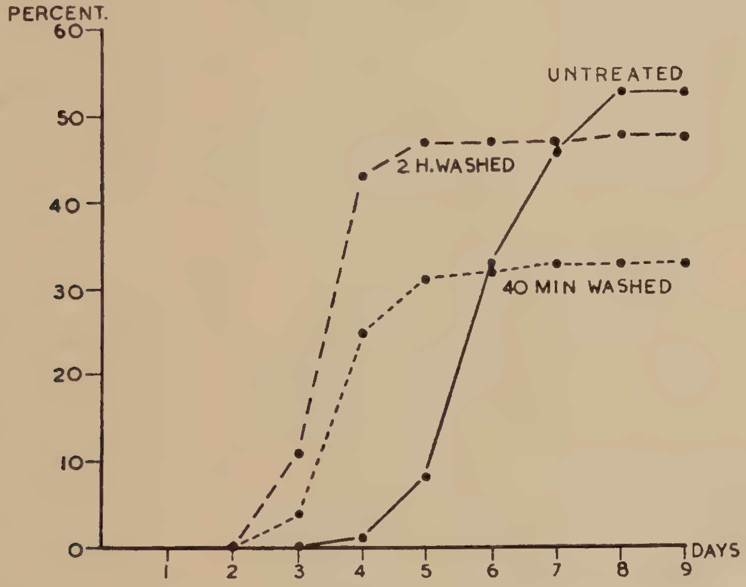

FIG. 6.

Germination of beet seed not disinfected: untreated; 40 minutes washed in running water; 2 hours washed in running water.

Another point which needs further investigation is the origin of nitrate in beet seed. That the nitrate content of plants is influenced by external conditions (light, temperature, water supply, mineral nutrition) is well known (Burström, 1946). In the experiments at Fonteinplaas, treatment with different fertilizers (superphosphate; F Mixture containing 4 per cent. N, 10 per cent. P_2O_5 and 3 per cent. K_2O; ammonium sulphate; ammonium nitrate) and different methods of harvesting and drying, had no significant effect on the nitrate content of the seeds, but more irrigation produced a lower nitrate content. This agrees with the results of Emmert (1936) with tomatoes. The content of other inorganic salts will be influenced likewise by external factors. This may be the clue to the statement by Visser (1945, p. 5) that sugar-beet seed contains varying quantities of germination inhibitors in different years, probably due to unknown climatic factors.

With regard to the correct method for the germination test with beet seed, disinfection should generally be used in addition to washing in running water. Both primary and secondary inhibitors are practically irrelevant to germination in soil so that their influence should be eliminated in the germination test. The following procedure is the best according to our experience :

(1) Washing in running tap water for 2 hours.
(2) Dipping in 0.5 per cent. Aretan solution for 20 minutes.
(3) Pouring off the Aretan solution and drying the seed, without its being washed, for at least 6 hours at room temperature.

To remove the primary inhibitors sufficiently, the time of washing should not be shorter than 2 hours. The time of dipping is not very important ; no significant differences were found when the seed was dipped for 10, 20 or 30 minutes in Aretan. Drying the seed, after the washing and dipping, accelerates the germination and facilitates the exact control of the water conditions in the germination dishes.

SUMMARY.

1. There are two types of germination inhibitors affecting beet seed :

(*a*) " Primary " substances, present in the dry seed.
(*b*) " Secondary " substances, formed during germination.

2. Free ammonia, which is a secondary inhibitor in beet seed, is formed mainly from nitrate by reduction.

3. Nitrite, an intermediate product of the nitrate reduction, does not act as germination inhibitor.

4. The reduction of nitrate is due to the action of bacteria which develop in large numbers on germinating beet seed.

5. In soil the formation of ammonia is harmless, but in the germination dishes it is inhibiting even in the smallest quantities.

6. By disinfection, the development of bacteria and the formation of ammonia can be prevented. It is therefore proposed to make the disinfection an official method for the germination test with beet seed.

7. Substances formed by micro-organisms are probably the cause of many irregularities observed in germination tests. These substances are mainly toxic but some may be stimulating.

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STUDIES OF FRUIT DEVELOPMENT IN RELATION TO PLANT HORMONES

I. HORMONE PRODUCTION BY THE DEVELOPING APPLE SEED IN RELATION TO FRUIT DROP

By **L. C. LUCKWILL**
Long Ashton Research Station, Bristol

SYNOPSIS

Measurements of the rate of fruit drop and the hormone content of the seeds, made at weekly intervals on three varieties of apple, have shown that periods of very active hormone production are invariably associated with periods of low fruit drop. On the basis of these and other observations, an hypothesis is proposed to account for the periodicity of fruit drop. It is suggested that, throughout its development, the fruit possesses an inherent tendency to separate from the spur but that, at certain periods, it is prevented from doing so by hormonal stimuli emanating from the developing seeds. Two such stimuli have been demonstrated, at 3-4 weeks and 7-10 weeks after petal-fall respectively, both of which are associated with particular developmental stages of the endosperm. In addition the existence of a third, as yet undetected stimulus at the time of fertilization, is postulated.

INTRODUCTION.

PREVIOUS work (Luckwill, 1948b) has demonstrated that the seeds of the apple at certain stages of development produce a hormone, extracts of which are active in inducing parthenocarpy in tomatoes and in delaying the abscission of ivy petioles cut short at ¼ in. from the stem. Investigations using the variety Beauty of Bath indicated the endosperm as the probable source of this hormone, and showed that the fluctuations in hormone production throughout the season were associated with definite stages in endosperm development. Further, there appeared in this variety to be some correlation between hormone production in the seed and the cessation of fruitlet abscission and, as a result of these experiments, it was suggested that the natural function of this endosperm hormone in the apple might be the control of fruit drop.

In view of the possible importance of this observation for an understanding of the fundamental causes and mechanism of fruit drop, it was thought desirable to repeat these experiments with other varieties of apple. The varieties used were Lane's Prince Albert and Crawley Beauty and, as in previous experiments, measurements were made of seed hormone production and rate of fruit drop at approximately weekly intervals from petal-fall till harvest. Observations were made also on seed and fruit development and the results were compared with those already obtained for Beauty of Bath.

EXPERIMENTAL METHODS.

Fruit drop measurements.

In the experiments with Lane's Prince Albert and Crawley Beauty, fruit drop was measured by spreading large hessian sheets (15 × 15 ft.) beneath the trees from which all the dropped fruits were collected at weekly intervals. The number of fruits dropped each week was then expressed as a percentage of the total number of fruits on the tree at the beginning of that week. Fruit drop was measured on two trees of each variety, of the same age and growing adjacent to the trees from which the seed samples were collected. Fruits which abscissed as a result of insect or fungal attack were counted separately and were disregarded in calculating the weekly rate of fruit drop, as were also unpollinated flowers which abscissed without showing any development of the ovary.

The fruit drop data for these two varieties thus differ somewhat from those already published for Beauty of Bath (Luckwill, 1948b), in which the drop was estimated at weekly intervals by counting the number of fruits remaining on marked branches and in which no differentiation was made between developing fruitlets and unpollinated flowers. In this variety, therefore, the abscission rate during the first two weeks after petal-fall appears much higher than it would have done had only the drop of developing fruitlets been measured. In other respects, however, the fruit drop data, presented graphically in Fig. 1, are comparable for all three varieties studied.

Seed and fruit measurements.

At weekly intervals a representative sample of fruits was collected from trees growing adjacent to those being used for the measurement of fruit drop. This was done by choosing a number of small branches distributed at random over the trees and stripping all the fruit from these branches. This method was found more satisfactory than attempting to pick individual fruits at random, as it eliminated what was otherwise a very strong tendency to select the largest fruits. Approximately 100 fruits were collected each week from petal-fall till harvest. After weighing and measuring, these were cut open and the seeds removed. The bulk of the seeds was immediately dried for hormone estimations, but a random sample of 50 was retained for measurements of seed and embryo length ; a further 25, after fixing in formalin-acetic-alcohol, were embedded in paraffin wax and sectioned at 15 μ. These sections, after staining in Delafield's haematoxylin and mounting, provided the material for a detailed study of embryo and endosperm development.

Hormone assay.

The method used for the measurement of the hormone content of the seed has been described in detail in previous publications (Luckwill, 1948a, b), and only a summary of the method will be given here :

The seeds, immediately on removal from the fruit, are dried in an oven at 100-120° C. and ground to a powder in a mortar. The following day, a weight of powder corresponding to 500 seeds is extracted with boiling water for 30 minutes and the water extract shaken with four changes of peroxide-free ether. The ether layer is separated and taken to dryness, and the residue dissolved in 1 ml. of hot distilled water. From this extract a series of five dilutions, corresponding to 500, 167, 50, 17 and 5 seeds per ml. of extract is prepared for testing. It has been estimated that this method of extraction removes between 50 and 60 per cent. of the total hormone content of the seed (Luckwill, 1948a).

The test method used depends on the ability of the active substance to stimulate parthenocarpy in the tomato (Luckwill, 1948a). It consists in adding a known quantity (0·0225 ml.) of each extract to a series of ten unpollinated tomato ovaries

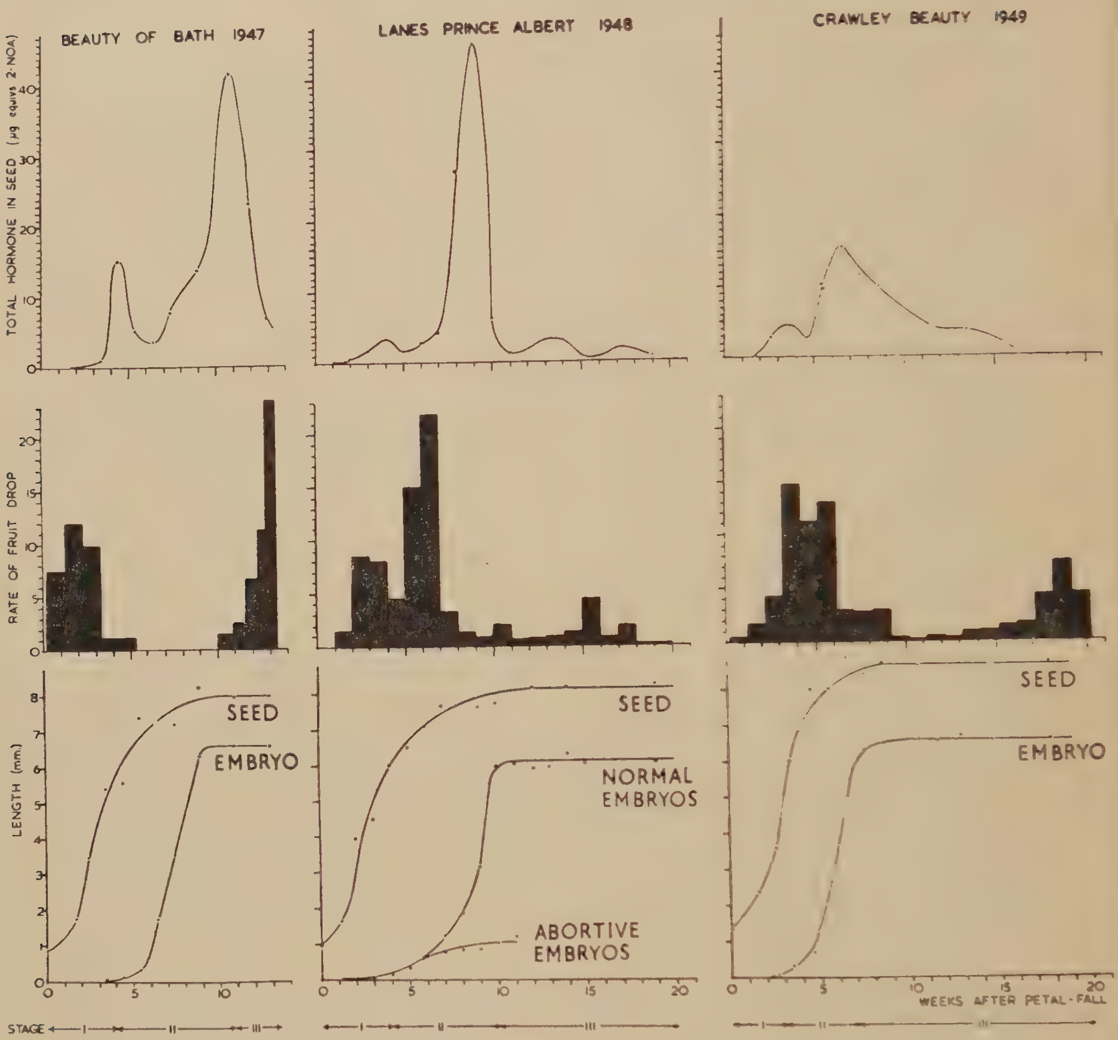

Fig. 1.

Graphs showing relation between hormone content of seed, rate of fruit drop, and growth of seed and embryo in three varieties of apple.

and measuring the resulting growth after a period of six days. By comparing the growth of the ovaries with that induced by known doses of the synthetic growth substance, 2-naphthoxy-acetic acid (2-NOA), the hormone content of the seed can be calculated in terms of microgram equivalents of 2-NOA.

Developmental stages of the seed.

The development of the seed in the apple normally proceeds in three well-defined stages to which, as they are closely associated with hormone production, it will be necessary to refer in the following paragraphs. These stages, which have been illustrated in a previous publication (Luckwill, 1948b), are briefly as follows :

Stage I. During this stage the central nucleus of the embryo-sac, having been fertilized by one of the male gametes, divides rapidly to form a large number of " free " endosperm nuclei which remain, unseparated by cell walls, embedded in a peripheral layer of cytoplasm. At the same time the fertilized egg-cell divides comparatively slowly to form a small spherical pro-embryo, attached by a suspensor to the wall of the embryo-sac. In most varieties of apple this free-nuclear stage of the embryo-sac persists for three to four weeks from the time of fertilization.

Stage II. The beginning of this stage is characterized by a sudden change from the free-nuclear to a cellular condition of the endosperm (cytokinesis), which now fills the embryo-sac. Simultaneously the embryo enters on a period of very rapid growth, and the cotyledons, plumule and radicle are differentiated. The primary endosperm is soon broken down and digested by the growing embryo and is replaced by a secondary endosperm tissue developed from a peripheral meristem. This secondary endosperm, too, is continually digested on its inner surface by the growing embryo within it, and is constantly regenerated by the meristem on its outer surface. The maximum volume of endosperm tissue is attained on the completion of embryo growth.

Stage III. During this stage the seed matures. No further growth of the embryo and endosperm occurs. The seed coat turns from white to brown and hardens as the seed dries out and enters its period of dormancy.

The duration of these three stages for the varieties under consideration is indicated in Fig. 1.

EXPERIMENTAL DATA.

Beauty of Bath, 1947.

In this variety no hormone could be detected during Stage I of seed development and there was a continual abscission of undeveloped flowers and young growing fruitlets (see Fig. 1). This was the " first " or post-blossom drop, and its sudden termination at the beginning of Stage II coincided with the appearance in the seed of relatively large quantities of hormone. Throughout Stage II, fruit drop was negligible, no typical " June " drop being observed in this variety. The heavy pre-harvest drop, which is characteristic of Beauty of Bath, occurred during Stage III at a time when the hormone content of the seed, having reached its maximum, was declining very rapidly (Luckwill, 1948b).

Lane's Prince Albert, 1948.

As in the previous variety, Stage I was characterized by an almost complete absence of hormone production by the seed and a high rate of fruitlet abscission (Fig. 1 and Table I). The first peak of hormone production again occurred at the beginning of Stage II, when the endosperm changed from the free nuclear to the cellular condition ; this peak was not nearly as marked as in Beauty of Bath, and it was not accompanied by the cessation of fruit drop. Its influence, however, may be reflected in the somewhat reduced rate of drop which occurred during the fifth week after petal-fall, a reduction which is considered to mark the limit between the " first " drop and the " June " drop. The termination of the " June " drop coincided with a period of very active hormone production by the seed between eight and ten weeks

Table I.

Lane's Prince Albert, 1948.

Days after petal-fall	Average diameter of fruit (mm.)	Seed length (mm.)	Embryo length (mm.)		Hormone content per 100 seeds (µg. equivs. 2-NOA)	Fruit drop % per week	Starch content of	
			Normal embryos	Abortive embryos			Pith	Cortex
0	3·7	0·95	—	—	—	0·0		
8	7·6	1·63	0·06	—	0·0	0·0		
12	—	—	—	—	0·0	0·0		
14	14·8	3·94	0·07	—	0·6	1·5		
21	19·7	4·47	0·09	—	1·5	8·5		
28	23·4	6·00	0·16*	—	3·5	8·0		trace
35	29·5	6·50	0·35	—	1·6	4·5		+
42	32·0	7·10	0·68	—	2·9	14·9		+
49	40·9	7·65	1·22	0·78	4·0	21·7		++
56	45·6	7·20	1·86	0·82	26·8	3·2	+	++
63	52·1	7·66	3·15	0·85	44·6	1·3	++	+++
70	60·0	7·70	5·99	1·04†	6·1	0·7	+++	+++
77	64·8	7·85	6·03	1·21	1·3	2·0	+++	+++
85	70·1	8·17	5·90	—	2·0	0·6	++	+++
91	65·1	7·90	5·95	—	3·1	0·6	++	+++
98	74·6	8·16	6·30	—	3·1	0·8	++	+++
105	69·6	8·18	6·03	—	0·9	1·3	+	+++
112	70·6	7·75	—	—	—	4·4	+	+++
119	66·1	7·65	—	—	1·8	0·7	+	++
126	78·4	7·75	—	—	—	1·9		++
133	77·4	8·25	6·06	—	0·7	0·2		++
136	77·6	—	—	—	—	0·2		++

* Cell wall formation in endosperm. † Collapse of endosperm in abortive seeds.

after petal-fall. After this, hormone production again fell and remained at a low level until harvest some ten weeks later. During this latter period there was nevertheless only a very low rate of fruit drop, and no definite pre-harvest drop was observed.

The major peak of hormone production in this variety appeared to be associated with embryo abortion, a phenomenon which was observed in approximately 80 per cent. of all the seeds examined. Seed development was normal in all the seeds up till the seventh week after petal-fall. During the eighth week it was apparent that some embryos were growing very much more slowly than others and, by the ninth week, the embryos of 80 per cent. of the seeds had virtually ceased their growth, although at that time they had attained only about one-twelfth of their full size. Endosperm development in these seeds, on the other hand, continued at about the normal rate until the tenth week and, since there was very little digestion of this tissue by the embryos, these abortive seeds, between the eighth and tenth weeks contained a much larger bulk of endosperm tissue than the normal seeds (Fig. 2). Although a direct comparison of the hormone content of normal and abortive seeds was not made, it is considered that this phenomenon might account for the exceptionally high hormone yields obtained from the seeds during this period, since it has been demonstrated that the highest concentrations of hormone invariably occur in the endosperm tissue. Towards the end of the tenth week these abortive seeds showed signs of collapse ; the endosperm suddenly shrivelled up, the seed lost its plumpness and became flattened, and the testas turned brown prematurely. This sudden

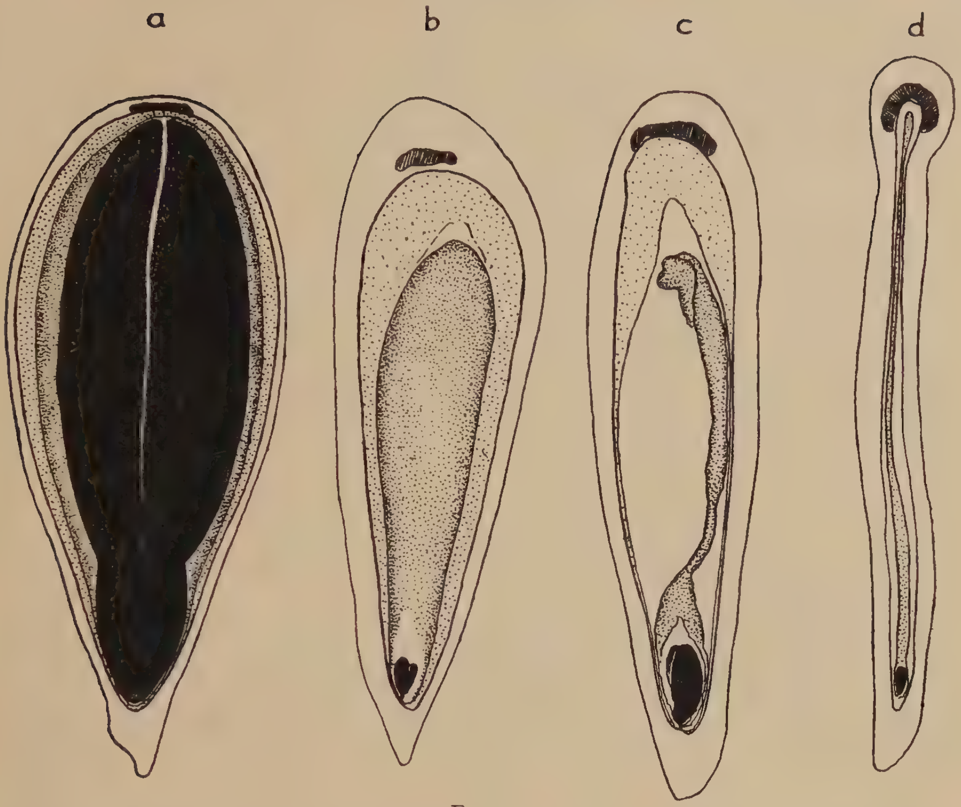

FIG. 2.

Seed abortion in Lane's Prince Albert, 1948. (*a*) L.S. normal seed, 9 weeks after petal-fall showing almost fully grown embryo surrounded by a layer of secondary endosperm tissue; (*b*) L.S. abortive seed, 9 weeks after petal-fall, showing embryo in a state of arrested development and abnormally large amount of endosperm; (*c*) abortive seed, 10 weeks after petal-fall, showing collapse of endosperm; (*d*) abortive seed, 12 weeks after petal-fall, showing collapse of whole seed. (Black = embryo; heavily stippled = endosperm; lightly stippled = nucellus; cross-hatched = sclerenchyma; unshaded = testa.)

collapse of such a large proportion of seeds was undoubtedly responsible for the sharp fall in hormone production which occurred during the tenth week, and for the subsequent very low values obtained in the hormone estimations. No explanation can be offered as to the cause of seed abortion in this variety in 1948. It is certainly not a phenomenon which occurs regularly in Lane's Prince Albert and on the same trees in 1949 and 1950 less than 5 per cent. of abortive seeds were found.

Fruits from controlled self- and cross-pollinations with a number of different pollens, carried out in 1949, all contained normal seeds: genetical causes therefore do not seem to be involved.

At the time of seed collapse, the fruits had already attained three-quarters of their final size and no marked effect on the course of fruit development was observed. There is, however, some evidence (Table II) that the fruits with the largest number of abortive seeds tended to reach a greater final size than those with fewer abortive seeds.

TABLE II.

Apple variety, Lane's Prince Albert.

Relationship between fruit size and percentage of seeds with abortive embryos.

	Fruit diameter (cm.).		
	Under 6·5	6·5-7·5	Over 7·5
No. of fruits examined ..	31	37	12
Average No. seeds per fruit ..	5·5	4·7	5·7
Per cent. abortive seeds ..	67·9	79·8	85·3

It seems likely that this correlation between the percentage of abortive seeds and fruit size may have a nutritional rather than a hormonal explanation, the food materials which normally would have been stored in the seeds having been diverted instead to the growing flesh of the fruit.

TABLE III.

Apple variety, Crawley Beauty, 1949.

Days after petal-fall	Average diameter of fruit (mm.)	Seed length (mm.)	Embryo length (mm.)	Hormone content per 100 seeds (μg. equivs. 2-NOA)	Fruit drop		Starch content of	
					Days after petal-fall	Drop % per week	Pith	Cortex
11	10·4	2·4	—	0·0	9	0·4		
18	16·1	3·6	0·09	2·8	16	1·7		
24	22·1	6·0	0·16*	4·5	23	4·2		
32	33·0	8·0	0·70	2·7	30	14·6		trace
37	—	—	—	10·1	37	11·2		
39	37·2	8·0	2·65	9·5	—	—	+	++
46	42·1	8·9	5·04	15·3	43	13·0	++	+++
53	44·7	8·4	6·24	11·5	51	3·0	+++	+++
60	51·3	8·7	6·28	9·8	58	2·7	++	+++
68	54·0	8·7	6·46	6·6	65	2·9	++	+++
74	54·6	8·6	6·59	—	72	0·4	++	+++
81	63·4	8·5	6·51	4·2	79	0·3	++	+++
90	64·3	8·7	6·68	—	86	0·5	++	+++
95	62·7	—	—	3·7	93	0·4	+	+++
102	67·5	8·6	6·55	—	100	1·0	+	++
109	70·3	—	—	1·5	107	1·0		++
—	—	—	—	—	114	1·4		
124	70·2	8·8	6·59	—	124	1·7		+
—	—	—	—	—	128	4·2		
—	—	—	—	—	135	7·3		
144	74·0	—	—	—	142	4·0		+

* Cell wall formation in endosperm.

Crawley Beauty, 1949.

The curve of hormone production by the seed throughout the season (Fig. 1) was similar in general form to that for the other varieties studied, showing two peaks at three and seven weeks after petal-fall, respectively. As in Lane's Prince Albert, the first peak was very low and had practically no effect on the course of fruit drop. The second and major peak, however, marked the end of the period of rapid fruit drop, seven weeks after petal-fall, although a limited amount of drop continued until the ninth week. During the maturing of the seed (Stage III), there was a steady fall in the hormone content until, at harvest, no further hormone activity could be detected in the seed extracts. Pre-harvest drop, which occurred from the 18th to 20th week after petal-fall did not show any close correlation with hormone production, which had already fallen to a very low level by the 16th week.

Seed development in this variety followed the normal course and the relationship between hormone production and endosperm development was much the same as that already established for Beauty of Bath. Very little hormone could be detected in the seeds during Stage I, whilst the endosperm was still in the free nuclear condition. Stage II was again characterized by an initial peak of hormone production, followed by a fall as the embryo started its period of rapid growth, and a subsequent rise to a second and higher peak on the completion of embryo growth. During Stage III, hormone production fell to zero though the fall was much more gradual than in Beauty of Bath, a difference which is probably associated with the much longer time taken for the seeds to mature in Crawley Beauty.

During the maturing of the seed it was noticed that, in addition to a gradual decline in the hormone content of the seed, there was a steady accumulation of growth inhibiting substances which, in the higher concentrations of seed extract, partially masked the activity of the hormone in the tomato ovary test. The distribution of these inhibiting substances in the mature seed and the possible part which they play in inducing dormancy, has been described in a recent publication (Luckwill, 1952).

It will be noticed from Fig. 1 that the hormone yields from the seeds of Crawley Beauty were generally lower than those obtained from either of the other varieties studied. It is thought that this is a varietal characteristic rather than a seasonal effect, since this variety also gave rather low yields in 1950.

Starch formation.

During 1948 it was noticed that the first appearance of starch in the developing fruits of Lane's Prince Albert coincided with the first peak of hormone production by the seed, and that the highest starch content was reached about one week after the highest hormone content (Table I). A somewhat similar relationship between seed hormone and starch production was found for Crawley Beauty in 1949 (Table III), but the significance of this relationship, if any, is not at present known. The observations of Ewert (1910) on the relationship between sugar content and seed number in pears suggests that the presence of seeds may in some way effect diastase activity in the fruit: on the other hand, the fact that starch first appears in the peripheral regions of the cortex, indicates that its formation is probably not controlled by any influence emanating from the seeds. Further investigation will be necessary before any conclusions on this point can be reached.

DISCUSSION.

The results presented in this paper show that the course of hormone production by developing apple seeds throughout the season varies considerably between different varieties in different years. The curves shown in Fig. 1, however, have certain important features in common: in all varieties the first 12 to 14 days after petal-fall are characterized by an absence of hormone production: the first peak for each variety occurs about three weeks after petal-fall, and corresponds closely with the time at which the endosperm passes from the free nuclear to the cellular condition (beginning of Stage II) ; and a second peak, which is always higher than the first, occurs in all three curves at, or just prior to, the completion of embryo growth. The latter is true both for Beauty of Bath and Crawley Beauty, in which embryo growth is normal, and for Lane's Prince Albert in which, in 1948, embryo growth was arrested at an early stage. In both types, the cessation of embryo growth is accompanied by optimum development of the endosperm.

The conclusions already reached regarding the relationship between seed, and particularly endosperm, development and hormone production are therefore confirmed by these further studies.

Regarding the suggested relationship between seed hormone production and fruit drop, it can be seen from Fig. 1 that periods of very active hormone production have invariably been associated with periods of low or negligible fruit drop. In all three varieties studied, the drop practically ceased as soon as the hormone content reached a value of about 10 μg. equivalents 2-NOA per 100 seeds, and usually remained at a low level for some weeks, even after the hormone content per 100 seeds had again fallen below this critical value. Thus, in Crawley Beauty, following a hormone peak of 15 μg. per 100 seeds, fruit drop remained low for six to eight weeks, whilst, in Lane's Prince Albert, a peak corresponding to 45 μg., although of short duration, was followed by a period of low fruit drop which lasted until harvest eleven weeks later. A similar effect can be seen following the first hormone peak in Beauty of Bath, though not following the second peak, which was followed closely by the pre-harvest drop. In addition, the data in Fig. 1 suggest that even minor peaks of hormone production (e.g. the first peak on the hormone curve for Lane's Prince Albert) may be followed by temporary reductions in the rate of fruit drop. The effect of these natural hormone stimuli, originating in the seeds, may thus be compared with that of synthetic growth substances such as α-naphthalene acetic acid, which, when applied in lanolin to the cut ends of defruited pedicels, delay abscission for a period which depends on the concentration used (Barlow, 1950).

Although these experiments do not prove conclusively that fruit drop is under the control of the hormone produced by the endosperm of the developing seed, they do provide circumstantial evidence in favour of such an hypothesis. There are, moreover, a number of previously established facts which, when considered together with the results of these more recent experiments, make this hypothesis even more likely. Thus, Heinicke (1917) established that those apples with the fewest seeds were the ones most likely to be shed during development, and this has since been confirmed by numerous other investigators ; further, it is known that the destruction of the seeds in a fruitlet, whether as a result of frost damage, insect attack or chemical treatment, is quickly followed by abscission of the fruitlet, and that such abscission can be delayed by the application of synthetic growth-substances.

Heinicke, in common with other investigators of fruit drop since the time of Langley (1729), assumed that the natural tendency of the apple was to remain attached to the parent bourse, and sought for the causes which, at certain stages of development, promoted its abscission, laying much stress on water relations and nutritional factors. Recent work would indicate, however, that throughout its growth the fruit possesses an inherent tendency to absciss from the tree and that it is only prevented from doing so as a result of hormonal stimuli originating in the fruit itself. The situation in the fruit is thus analogous to that in deciduous leaves, where the continued attachment of the leaf to the stem seems to be dependent on the ability of the lamina to maintain a supply of " auxin " passing down the petiole. Hormone production in the fruit, however, differs from that in the leaf in being a discontinuous rather than a continuous process, and it is considered that in this fact lies the fundamental cause of the periodicity which is a characteristic feature of fruit drop in the pome and stone fruits.

In the apple, two principle phases of hormonal stimuli, emanating from the developing seeds, have been demonstrated. The first of these, which occurs three to four weeks after petal-fall at the time of cell wall formation in the endosperm, marks the end of the " first drop ". A second and much stronger stimulus at the time of completion of embryo growth, seven to ten weeks after petal-fall marks the end of the " June drop ", and it seems probable that the effect of this stimulus persists until the start of the pre-harvest drop.

In addition to these two hormonal stimuli, which have been demonstrated experimentally, it is necessary to postulate the existence of a third stimulus at the time of fertilization, which is responsible for the initiation of fruit development and for the first period of reduced abscission ten to fourteen days after fertilization. The existence of such a stimulus to growth, associated with the act of fertilization, has been demonstrated experimentally for a number of plants, and it seems highly probable that it occurs also in the apple. The fact that extracts of very young apple seeds are inactive in inducing parthenocarpy in the tomato, however, suggests that this initial hormone stimulus is of a different nature from that of the two subsequent ones which have been studied in the experiments reported above or, alternatively, that it has its origin in some tissue outside the seed. These views, which should be regarded as a working hypothesis, rather than as the final solution of the problem of fruit drop, are illustrated diagrammatically in Fig. 3.

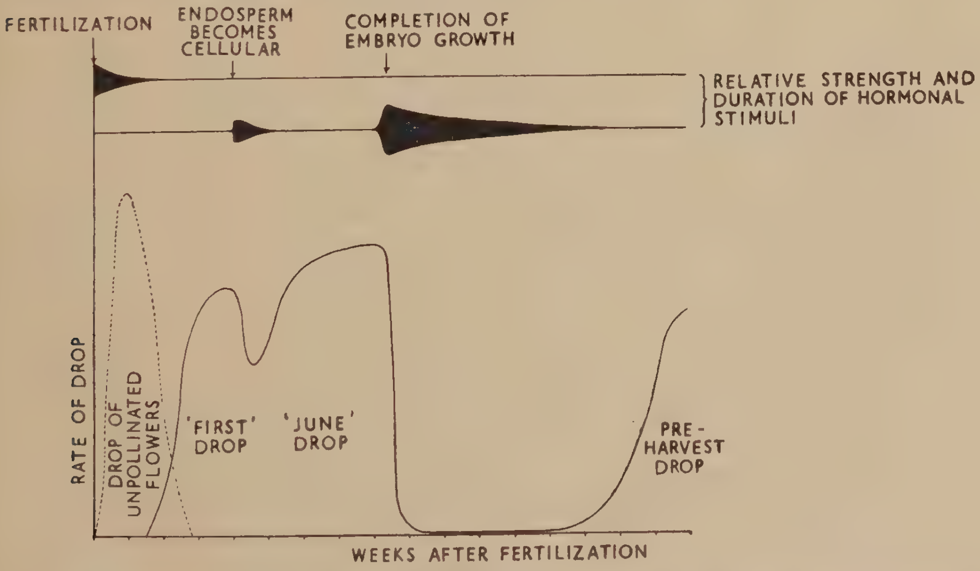
FERTILIZATION
ENDOSPERM BECOMES CELLULAR
COMPLETION OF EMBRYO GROWTH
RELATIVE STRENGTH AND DURATION OF HORMONAL STIMULI
RATE OF DROP
DROP OF UNPOLLINATED FLOWERS
'FIRST' DROP
'JUNE' DROP
PRE-HARVEST DROP
WEEKS AFTER FERTILIZATION

FIG. 3.

Diagram illustrating the hypothesis proposed to account for the periodicity of fruit drop in apples (see text).

SUMMARY.

1. Measurements were made of the hormone content of the seed and the rate of fruit drop at approximately weekly intervals from petal-fall till harvest in the apple varieties Lane's Prince Albert and Crawley Beauty. Parallel observations were made also on seed and fruit development and the results compared with those already published for Beauty of Bath (Luckwill, 1948b).

2. As in Beauty of Bath, the first peak of hormone production in both these varieties occurred at the time of cell wall formation in the endosperm, three to four weeks after petal-fall.

3. A second and much more marked peak occurred at or just prior to the completion of embryo growth, at the time when the endosperm reached its optimum development.

4. Seed development in Beauty of Bath and Crawley Beauty followed the normal course but, in Lane's Prince Albert in 1948, embryo growth in 80 per cent. of seeds was arrested at an early stage of development, due to unknown causes. Such seeds later aborted. Fruits with the most abortive seeds tended to reach a greater final size than those with fewer abortive seeds.

5. In Lane's Prince Albert and Crawley Beauty, the first appearance of starch in the fruit coincided approximately with the first peak of hormone production by the seeds. The optimum starch content was reached about one week after the optimum hormone content.

6. In all three varieties, periods of very active hormone production were associated with periods of low or negligible fruit drop. The period over which fruit abscission was inhibited seemed to depend on the strength of the hormone stimulus emanating from the seeds.

7. On the basis of these and other observations, a working hypothesis is proposed to account for the periodicity of fruit drop in apples.

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STUDIES OF FRUIT DEVELOPMENT IN RELATION TO PLANT HORMONES

II. THE EFFECT OF NAPHTHALENE ACETIC ACID ON FRUIT SET AND FRUIT DEVELOPMENT IN APPLES

By L. C. LUCKWILL
Long Ashton Research Station, Bristol

SYNOPSIS.

The experiments described in this paper were designed: (1) to investigate the mechanism whereby α-naphthalene acetic acid (NAA), applied as a spray to apple trees between full bloom and two to four weeks after petal-fall, reduces the crop; and (2) to assess the possible value of this substance as a blossom- and fruit-thinning agent.

Spraying open flowers with NAA before pollination was found to induce incompatibility between the pollen tubes and the stylar tissue, and it is considered that this may account for the reduction in set which results from spraying trees at full bloom with NAA. Applied after petal-fall, the spray caused the abortion of a large proportion of the developing seeds and this, in turn, led to an abnormally large drop of young fruitlets. The seeds appeared to be susceptible to damage by NAA only as long as the endosperm was in the free nuclear stage, a condition which, in most varieties of apple, persists until about the third week after petal-fall. As a thinning agent, NAA has the disadvantage that it tends to retard fruit growth. This effect is particularly marked when the spray is applied later than two weeks after petal-fall, and frequently offsets any increase in fruit size which might have resulted from thinning. Earlier application of the spray may, in certain varieties, cause a permanent stunting of the foliage. In the strongly biennial Miller's Seedling, none of the thinning treatments, using NAA on individual branches, resulted in the differentiation of fruit buds in the " on " year.

INTRODUCTION

In 1941 Burkholder and McCown (1941) reported experiments in which halves of Starking apple trees were sprayed at full bloom with α-naphthalene acetic acid in an attempt to increase the set of fruit. Contrary to expectation, this treatment was found to decrease rather than increase fruit set. Similar reductions in fruit set were obtained by Greene (1943) as a result of smearing the pistils of Starking apples with lanolin pastes containing NAA and other growth substances and also by spraying the open flowers with wax emulsions containing 3,000 p.p.m. NAA. More recent work (Luckwill, 1949) has shown that concentrations of NAA and indolyl-acetic acid as low as 5 p.p.m. are effective in reducing fruit set of apples and that 2 : 4 dichlorophenoxyacetic acid is active at only 1 p.p.m. when applied at full bloom.

These results have drawn attention to the possibility of using NAA or other synthetic growth regulators as thinning agents to increase fruit size and quality in those apple varieties which normally carry heavy crops, and to encourage regular annual cropping in varieties which would otherwise tend to bear biennially.

Davidson *et al.* (1945) were the first to show that NAA was effective as a thinning agent, not only at full bloom but also when it was applied after bloom, up to a period of about three weeks after petal-fall. Beyond this date, application of NAA was without effect on fruit set, though Southwick and Weeks (1949) later showed that Golden Delicious could be thinned with NAA as late as four weeks after petal-fall.

Within the past six years a number of workers in the United States have carried out trials to compare the effectiveness of NAA, as a thinning agent for apples, with that of other materials which have been recommended for the same purpose, particularly dinitro-o-cyclohexyl phenol and sodium di-nitro-o-cresylate. Murneek (1950), in a recent review of these trials, concludes that NAA has decided advantages over the DN compounds. The latter have to be applied at full bloom or shortly afterwards, at which time the foliage is particularly sensitive to spray injury and is often permanently damaged. NAA, on the other hand, can be used with equal effectiveness one to three weeks after petal-fall when the foliage is much more resistant and the thinning requirements can be determined with greater certainty.

Post-blossom applications of NAA are known to reduce fruit set by increasing the drop of young fruitlets, but the American investigators offer no explanation of why this substance, applied at one stage of development, promotes fruit drop whereas, at another stage of development, it prevents it. Neither is it known how the treatment of open blossoms with growth substances reduces fruit set since, at the very low concentrations which are necessary, no visible damage to the floral parts occurs. It was primarily in order to investigate further the mechanism of the action of NAA on fruit set that the present series of experiments was planned, though at the same time it was hoped to obtain information regarding the practical possibilities of the method for regulating fruit set and controlling biennial bearing in certain English varieties of apple.

Of the apple varieties used in these experiments Miller's Seedling is strongly biennial in habit and consistently sets a very heavy crop in its " on " year which needs drastic thinning in order to produce fruit of marketable size. Emneth Early (syn. Early Victoria) is also a biennial bearer, though not to the same extent as Miller's Seedling, and frequently crops so heavily as to make thinning necessary. Crawley Beauty shows little tendency to biennial bearing and regularly carries heavy crops of rather small fruits. Thinning in this variety has been observed to produce a very marked increase in fruit size.

EXPERIMENTAL DATA.

EXPERIMENT 1—MILLER'S SEEDLING.

Method.

In this experiment, NAA at a uniform concentration of 20 p.p.m. in water, was sprayed on branches of Miller's Seedling in their " on " year at six different dates from pink-bud to forty-one days after petal-fall. Control branches were unsprayed.

The seven treatments were randomized amongst forty-two large branches on ten mature bush trees, giving six replications per treatment. Of the six branches sprayed at each stage of development, three received NAA only and three NAA + wetter (0·25 per cent. " Teepol "). Preliminary analysis of the data showed that the addition of wetter had no influence on the effectiveness of the spray, so that in all subsequent calculations the " with " and " without wetter " series have been combined. Details of the dates of spraying, stage of blossom or fruit development and notes on the weather at the time of spraying are set out below.

Effect on fruit set and fruit drop.

The number of blossom-buds on each of the experimental branches was counted at bud-burst, and later records were made of the number of fruits set on each branch.

Date of spraying	Stage of development	Weather at time of spraying
22.4.50	Pink-bud	Calm, sunny, warm.
2.5.50	Full-bloom	Sunny, warm, very windy.
12.5.50	Petal-fall	Sunny, very hot, strong breeze.
19.5.50	Petal-fall+7 days	Dull, warm, thundery; heavy shower 2½ hours after spraying.
6.6.50	Petal-fall+25 days	Sunny, very hot, slight breeze.
22.6.50	Petal-fall+41 days	Cool, breezy; light shower ½ hour after spraying.

"*Initial*" *set* refers to the number of swelling fruitlets counted fourteen to eighteen days after petal-fall, before the start of the first drop but after the abscission of unpollinated flowers; it therefore represents the number of flowers effectively pollinated. "*Final*" *set* was recorded after the completion of the "June" drop, when the fruits were approaching maturity. In both instances the set is expressed as the number of fruits per 100 blossom clusters. The difference between initial and final set represents the number of fruitlets dropped, which is expressed as a percentage of the initial set.

The records for final set given in Table I show that the application of NAA at al stages between full bloom and twenty-five days after petal-fall resulted in a very marked fruit thinning, whilst spraying at pink-bud or as late as forty-one days after petal-fall had no effect on fruit-set.

The data also reveal that this thinning effect may result from one of two causes. When NAA is applied at full bloom a very large proportion of the flowers fail to show any development and, after the temporary abscission-delaying effect of the spray has worn off, these undeveloped flowers are shed; the remaining fruitlets develop normally though they show a somewhat reduced drop. The effect of the spray here has evidently been to prevent fertilization in a large proportion of the flowers. With post-blossom applications, on the other hand, the thinning is achieved as the result of an increased drop of developing fruitlets. When NAA was applied at petal-fall, both these causes contributed to the thinning effect, as is indicated by the decreased initial set and by the increased drop.

At all stages of development the spray had a temporary inhibiting effect on abscission and no drop occurred for a period of one to three weeks following each application. This is in accordance with the well-known effect of NAA in delaying the development of the abscission layer, an effect which is used in the control of pre-harvest drop. Some evidence was obtained that the eventual heavier drop from branches receiving post-blossom applications of NAA might be associated with an increased degree of seed abortion. Seed counts on fruits harvested at the end of the season showed that, although the total number of seeds per fruit was about the same for all treatments, there was a marked increase in the percentage of abortive seeds in fruits from branches sprayed between petal-fall and petal-fall + 25 days (Table I). These abortive seeds were almost as long as the fully developed seeds but were flat and shrunken and devoid of embryo and endosperm.

Effect on fruit size.

In order to determine the effect of the various spray applications on fruit size, a random sample of 200 fruits from each treatment was taken. The fruits were

TABLE I.

Effect of NAA (20 p.p.m.) sprayed at different stages on branches of apple variety Miller's Seedling.

Stage when sprayed	No. of blossom clusters	Fruit set per 100 blossom clusters		Fruit drop as % of initial set	Mean fruit weight (gm.)	% fruits of diameter		Total crop per 100 clusters (kg.)	% abortive seeds at harvest
		Initial	Final			less than 2 in.	more than 2 in.		
Control unsprayed . .	1,790	242±15	61± 3·6	75	38·6±0·68	90·5	9·5	2·35	27·2
Pink-bud . .	1,348	254±17	59±12·0	77	**49·3**±1·21	60·5	39·5	2·91	20·1
Full-bloom . .	1,419	**60**±14	**24**± 7·7	60	**49·5**±1·08	57·5	42·5	1·19	17·5
Petal-fall . .	1,663	**158**±29	**24**± 6·6	85	**53·4**±0·91	41·0	59·0	1·28	30·1
Petal-fall +7 days . .	1,552	250±21	**27**± 5·4	89	**51·4**±1·10	50·0	50·0	1·39	36·0
Petal-fall +25 days . .	802	278±24	**22**± 7·2	92	**29·5**±0·65	100·0	0·0	0·65	50·5
Petal-fall +41 days . .	709	244±14	53± 6·1	78	37·9±0·75	88·0	12·0	2·01	26·6

Note.—Means in bold figures are those which differ significantly from the control. The difference exceeds 2 × S.E.

weighed individually and hand graded into two size categories with the results shown in Table I.

The applications of NAA between full bloom and seven days after petal-fall were all effective in increasing fruit size, which was to be expected in view of the heavy thinning achieved. Branches sprayed 25 days after petal-fall, however, although they were thinned to about the same degree as those sprayed at petal-fall, yielded only " chat " fruits, all of which were less than 2 in. in diameter. Application of NAA at this particular stage of development obviously had a very potent inhibiting effect on fruit development, which was possibly associated with the high percentage of seed abortion noted. Applied at 41 days after petal-fall, the spray had no significant effect on the percentage set, on the percentage of abortive seeds or on fruit size.

An unexpected result was the considerably enhanced fruit size resulting from the application of NAA at pink-bud. Although this spray had no significant thinning effect it appears to have increased fruit weight by as much as 28 per cent. over that of the unsprayed controls. Here again, it is perhaps significant that the percentage of abortive seeds was less than in the control sample.

Effect on foliage.

The application of NAA at full bloom resulted in a marked stunting of the spur foliage which persisted throughout the season. The leaves were small and many were " cupped " at the tip. Few new leaves were produced following the spray application. At pink-bud and petal-fall the damage was less severe than at full bloom. Where the application was delayed until seven days after petal-fall or later, no permanent damage to the foliage was noticeable.

Effect on fruit bud formation.

Examination of the experimental branches in the spring of the following year revealed that none of the thinning treatments applied had been effective in inducing fruit-bud formation. This does not necessarily imply that NAA applied as a thinning spray to whole trees would not be effective in causing flowering in the " off " year, since it is well known that the factors controlling fruit-bud formation are not localized in individual spurs or branches. Nevertheless it is to be expected that the serious reduction in leaf area which occurs with the early thinning treatments would itself have an adverse effect on the differentiation of fruit buds.

EXPERIMENT 2—EMNETH EARLY.

Method.

In this experiment, as in the previous one, NAA was used at a concentration of 20 p.p.m. in water, with the addition of 0·25 per cent. " Teepol " as a wetting agent. The spray was applied to individual branches of Emneth Early at six stages of development ranging from green-cluster to two weeks after petal-fall, using a small hand pump. Control branches remained unsprayed.

Each of the seven treatments was applied to five branches, i.e. 35 branches in all, which were distributed at random amongst eight trees. The trees had borne a fairly heavy crop the previous year and were carrying only a moderate number of blossom buds. The blossoming season was an exceptionally lengthy one, the flower buds opening irregularly over a period of nearly four weeks ; consequently the flowering stages named in Table II must be regarded only as approximate statements of the average state of the buds. This exceptional variability in the time of flowering was undoubtedly responsible for the high standard errors of the fruit-set means (Table II).

Effect on fruit set.

In this experiment only the final set of fruit was measured, i.e. after the cessation of the " June " drop. As can be seen from Table II, application of NAA at early bloom eliminated practically the entire crop, and thinning was also heavy when the spray was applied one week later, approximately at the stage of full bloom. The petal-fall application reduced the crop to about half, but no significant thinning was achieved by spraying at 14 days after petal-fall. This is in marked contrast to Miller's Seedling where it was possible to thin with NAA as late as 25 days after petal-fall. The marked reduction in set which followed the spray application of 2nd May (approximate stage of pink-bud) was probably due to the fact that many of the flower buds had already opened on this date, as the evidence from other experiments suggests that NAA does not prevent setting when it is applied to unopened flower buds.

TABLE II.

Effect of NAA (20 p.p.m.), applied at different times, on fruit set and fruit weight of Emneth Early.

Date of spraying and condition of tree	Weather at time of spraying	No. of blossom clusters	Final fruit set per 100 clusters Mean	Fruit weight (gm.) Mean
Control unsprayed	—	1,147	56±6·4	90·4±4·30
14.4.50 Green cluster	Dull, cool, slight breeze	223	52±20·5	82·8±2·50
2.5.50 Pink-bud	Warm, sunny, windy	188	**22**±10·3	— * —
4.5.50 Early bloom	Warm and sunny	231	**3**± 1·5	— * —
11.5.50 Full bloom	Hot, sunny, slight breeze	866	**16**± 6·3	90·4±4·76
17.5.50 Petal-fall	Cold, dry, windy	235	**26**± 9·5	**62·9**±4·46
31.5.50 Petal-fall +14 days	Warm and sunny	281	44±18·1	**49·8**±5·33

* Owing to a severe attack of brown-rot and to heavy pre-harvest drop, insufficient fruits were harvested from these branches to provide a reliable estimate of fruit weight.

Note.—Means in bold figures are those which differ significantly from the control. The difference exceeds 2 × S.E.

Effect on fruit size.

As can be seen from Table II, the marked thinning achieved by the spray application at full bloom in this variety did not result in an increase in fruit size. This is probably due to the fact that the unthinned control trees themselves were carrying only a moderate crop for, although the set per 100 blossom clusters was about the same as in Miller's Seedling, there were far fewer blossom buds per unit length of branch, the trees being in their " off " year. The applications at petal-fall and petal-fall + 14 days, on the other hand, gave fruits which were obviously much smaller than those from the control branches, thus confirming the impression gained from the previous experiment that post-blossom applications of NAA have a direct inhibiting effect on fruit growth.

Effect on foliage and fruit-bud formation.

The foliage of Emneth Early appeared considerably more resistant to NAA than that of Miller's Seedling and, apart from a slightly " wilted " appearance lasting for four or five days following spraying, no damage was observed. Both control and sprayed branches formed abundant fruit-buds and flowered normally the following spring (the " on " year).

EXPERIMENT 3—CRAWLEY BEAUTY.

Method.

This experiment was designed to obtain further information on the effect of post-blossom applications of growth-substances. NAA at two different concentrations (20 and 50 p.p.m.) was sprayed on to large branches of twelve mature bush trees at four different times between petal-fall and petal-fall + 30 days. Each of the eight spray treatments was applied to four replicate branches and, in addition, there was one unsprayed control branch on each tree, making a total of 44 branches.

All the trees flowered profusely and, as is usual with this variety at Long Ashton, set a very heavy crop of fruitlets, the " initial " set averaging 260 fruitlets per 100 blossom clusters. The first spray was applied on 9th June when practically all the petals had dropped and the first fruitlets were just beginning to swell ; ten days later, when the second spray was put on, unpollinated flowers were dropping but the first drop of growing fruitlets had not yet started. Twenty days after petal fall, when the third spraying was made, the first drop was occurring. The last sprays were applied on 8th June, 30 days after petal-fall, by which time the " June " drop was well under way. In this experiment all the sprays were applied under good weather conditions and no rain fell within 24 hours of spraying.

Effect on fruit set.

Crawley Beauty was found to be more sensitive to NAA than was either of the other varieties investigated. Application of 20 p.p.m. at petal-fall eliminated over 90 per cent. of the crop and caused severe damage to the spur leaves. Leaves already developed became cupped and distorted and the development of new leaves was greatly retarded. At 50 p.p.m. the damage was even more severe.

At ten days after petal-fall the 20 p.p.m. spray thinned the crop to about the right amount and there was practically no foliage damage. Where 50 p.p.m. was used the crop was again over-thinned and development of the spur leaves slightly checked. When sprayed at 20 days after petal-fall, less thinning was achieved but no damage was caused to the foliage either by the 20 p.p.m. or by the 50 p.p.m. spray. Ten days later, when the June drop was just starting, neither spray had any significant effect on fruit set or on foliage development (Table III). Microscopic examination showed that by this stage practically all the seeds had formed a cellular endosperm, whereas at the time of the previous spraying (20 days after petal-fall) all the endosperms examined were in the free-nuclear condition. Previous work (Luckwill, 1953) has led to the conclusion that the change from the free-nuclear condition to the cellular condition in the endosperm is an event of great physiological significance in the development of both the seed and the fruit, and it is suggested that this change may define the critical limit beyond which synthetic growth-substances are without effect on seed development and fruit set.

TABLE III.

Effect of post-blossom sprays of NAA on fruit set and fruit size in apple variety Crawley Beauty.

Conc. of NAA (p.p.m.)	Stage when sprayed	No. of blossom clusters	Final set per 100 clusters	Average fruit weight (gm.)	% "king" fruits harvested
0	Control	2,593	63±4·5	72± 1·6	13·4
20	Petal-fall	931	**6**±1·7	99±14·9	17·4
,,	,, +10 days	1,246	**15**±3·3	**90**± 4·0	17·1
,,	,, +20 days	988	**35**±3·8	**59**± 6·0	11·8
,,	,, +30 days	890	62±3·9	**55**± 3·3	9·0
50	Petal-fall	977	**3**±2·0	111±19·8	10·5
,,	,, +10 days	1,152	**9**±1·8	70± 5·9	17·5
,,	,, +20 days	1,118	**26**±5·0	**55**± 3·6	8·0
,,	,, +30 days	1,076	63±5·7	**55**± 2·3	9·0

Note.—Means in bold figures are those which differ significantly from the control. The difference exceeds 2 × S.E.

Effect on fruit size.

As with Miller's Seedling and Emneth Early, NAA proved to have a strong inhibiting influence on the growth of the fruit. This was most clearly seen on branches, sprayed 30 days after petal-fall, which carried a heavy crop of obviously undersized fruits; these, however, ripened normally and were ready for harvest at the usual time. Where the 20 p.p.m. spray was applied within ten days of petal-fall, fruit weight was significantly increased, the thinning effect predominating over the direct inhibiting action. These interacting effects are shown graphically in Fig. 1.

Proportion of "king" fruits in crop.

On branches which had been heavily thinned with NAA, the proportion of terminal ("king") fruits tended to be slightly higher than on the control branches. As the figures in Table III show, however, this was not invariably so, and in no case did the differences between the treated and control branches reach the level of statistical significance.

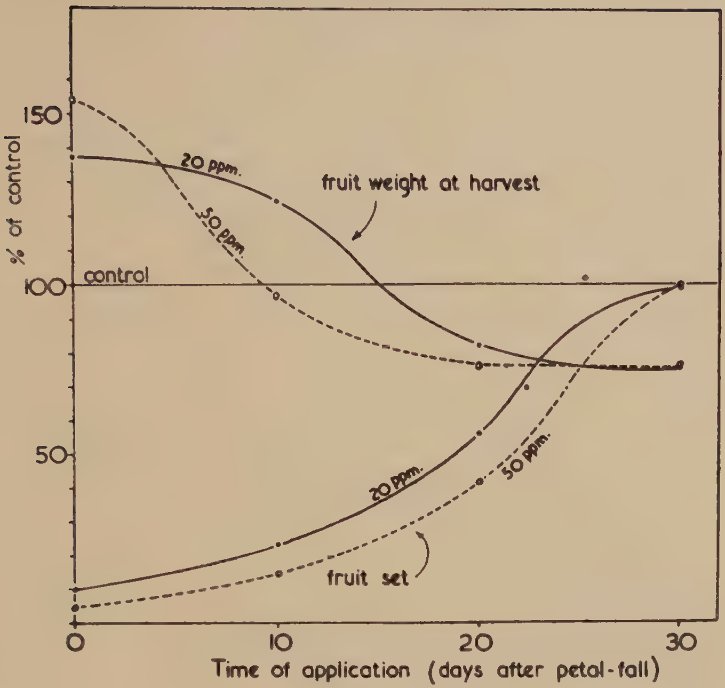

FIG. 1.

Graph showing the effect of time of application of NAA sprays (at concentrations of 20 and 50 p.p.m.) on fruit set and average fruit weight at harvest in the apple variety Crawley Beauty. Both fruit weight and fruit set have been expressed as a percentage of the mean fruit weight and fruit set on the unsprayed control trees.

EXPERIMENT 4—CRAWLEY BEAUTY.

Method.

This experiment was of a type different from the three already described. Its purpose was to study in more detail the effect of NAA, applied at petal-fall, on the development of the seed and the fruit, and on fruit drop, from week to week throughout the season. Four mature bush trees of Crawley Beauty were chosen, as nearly as possible of the same size and stage of development, and carrying approximately the same number of blossom buds. Trees 1 and 3 were controls which received no treatment, whilst trees 2 and 4 were sprayed with 40 p.p.m. NAA at petal-fall. A rather high concentration of NAA was purposely used in this experiment in order to exaggerate the effects it was desired to study.

From trees 1 and 2, samples of 50 fruits were gathered each week, using the method already described (Luckwill, 1953), and measurements were made of mean fruit weight, seed number and percentage of abortive seeds. No fruits were picked from trees 3 and 4 but, at weekly intervals, all the dropped fruits were collected from large hessian sheets spread beneath the trees.

Effect on cropping.

A comparison of the records for trees 3 and 4 (Table IV) shows that the petal-fall spray of 40 p.p.m. NAA reduced the crop by approximately 80 per cent. and that this was achieved mainly as a result of an increased drop. There was also a small reduction in the initial set, due probably to the fact that at the time of spraying some blossom clusters were still at full bloom. Although the total crop on the sprayed tree was very much smaller than that on the control, fruit size was greatly enhanced as a result of the thinning achieved. Examination of the weekly fruit weight averages in Table V, however, reveals that for the first five weeks the sprayed fruits were actually smaller than the controls. By the sixth week after spraying, the crop had been heavily thinned and the growth rate of the remaining fruits increased so rapidly that they soon overtook the controls.

TABLE IV.

Effect of NAA (40 p.p.m.), applied at petal-fall, on cropping of apple variety Crawley Beauty.

		TREE 3 Control—not sprayed	TREE 4 Sprayed NAA 40 p.p.m. at petal-fall
a	No. of blossoms on tree . .	12,984	15,705
b	Initial no. fruits set . .	7,147 (55% of a)	7.053 (45% of a)
c	No. fruits dropped	5,032 (70% of b)	6,793 (96% of b)
d	No. fruits picked	2,115 (30% of b)	260 (4% of b)
e	Average fruit weight (gm.) . .	58	117
f	Total crop (kg.)	122·5	30·4
g	Crop per 1,000 blossoms (kg.)	9·45	1·93

Seed abortion and fruit drop.

The experiment with Miller's Seedling suggested that the increased drop, following post-blossom applications of NAA, might be associated with an increased degree of seed abortion and this conclusion is fully confirmed by the results presented in Table V. In the third week after petal-fall, for instance, 92 per cent. of the seeds on the sprayed trees had ceased to grow and were aborting, compared with only 6 per cent. on the unsprayed control trees. The following week there was an exceptionally heavy drop of fruitlets from the sprayed trees and there seems little doubt that there exists a direct causal relationship between these two events. The close correspondence between seed abortion and fruit drop is illustrated in Fig. 2, where the extra drop resulting from spraying (weekly per cent. drop from sprayed tree less that from control tree) is plotted, together with the per cent. of abortive seeds found in samples of sprayed fruitlets during each successive week. It will be seen that the two curves are very similar in general form, but that there is a lag period of approximately one week, which may be interpreted as the time required for the development of the abscission layer after the seeds have aborted. It will be noticed from this diagram that although NAA was applied at petal-fall, the actual thinning did not take place until the fourth to seventh week after petal-fall.

Microscopic examination of aborting seeds from fruitlets sprayed with NAA at petal-fall showed that the first tissue to be affected was the nucellus, the cells of which showed signs of collapse within 14 days of spraying. Destruction of the nucellus was followed by a cessation of growth and eventual necrosis of the embryo and

TABLE V.

Effect of NAA on the weekly percentage of fruit drop, growth of fruit and seed abortion in Crawley Beauty.

Weeks after petal-fall	Control unsprayed			Sprayed NAA 40 p.p.m. at petal-fall			Extra % fruit drop resulting from spraying
	Weekly % drop	Average fruit weight (gm.)	% abortive seeds	Weekly % drop	Average fruit weight (gm.)	% abortive seeds	
1	0·0	0·46	0·0	0·0	0·32	0·0	
2	0·0	1·09	2·9	0·0	0·45	27·8	
3	11·3	2·28	6·1	11·5	0·59	92·7	0·2
4	37·7	5·68	13·4	73·5	1·49	91·5	35·8
5	13·9	7·88	12·0	42·9	5·82	62·4	29·0
6	14·0	12·2	3·3	43·8	13·7	11·0	29·8
7	16·5	19·1	4·4	27·6	21·7	3·9	11·1
8	7·3	25·6	2·8	7·8	34·5	6·4	0·5
9	1·9	24·0	4·1	5·7	40·9	3·6	3·8
10	0·8	31·0	2·4	10·8	47·8	2·5	10·0
11	0·4	34·2	1·5	0·0	56·3	3·9	—0·4
12	0·2	44·7	3·6	1·0	81·3	3·0	0·8
13	0·0	52·8	10·0	3·0	82·7	5·3	3·0
14	0·6	58·4	3·1	3·4	84·2	8·2	2·8
15	0·5	66·0		3·2	97·1		2·7
16	0·2	71·0		0·0	101·2		—0·2
17	0·3	75·5		0·0	105·8		—0·3
18	2·0	76·2		4·0	108·4		2·0

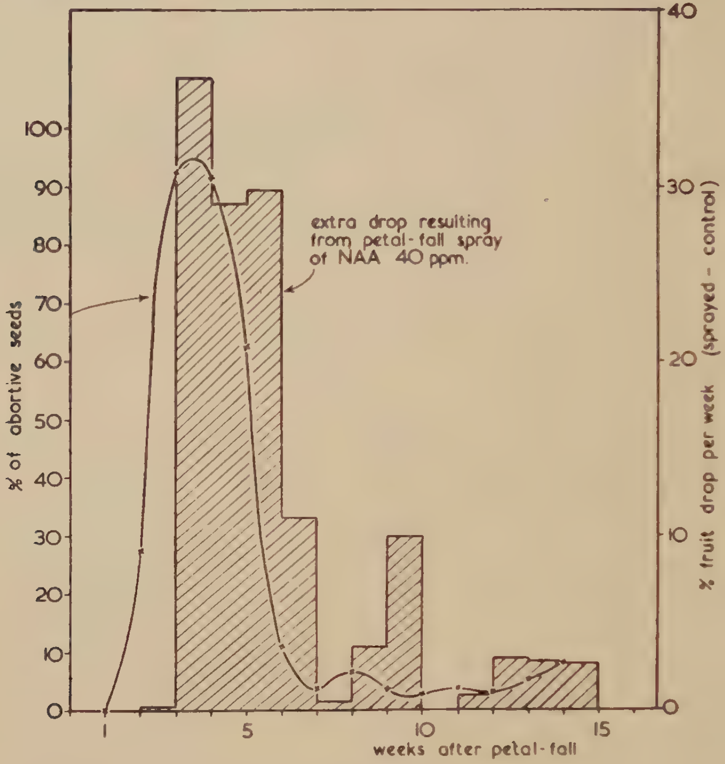

FIG. 2.

Diagram showing the percentage of abortive seeds in samples of fruit taken at weekly intervals from a tree of Crawley Beauty sprayed at petal-fall with NAA 40 p.p.m. (smooth curve), and the extra fruit drop induced by the spray (shaded histogram).

endosperm. Cell wall formation in the endosperm was greatly delayed and, in the majority of seeds examined, had not been completed before the death of endosperm and the total collapse of the seed.

EXPERIMENT 5—EFFECT OF NAA ON POLLEN TUBE GROWTH.

Experiment 1 indicated that when NAA at a concentration of 20 p.p.m. is sprayed on to apples at full bloom a large proportion of the flowers drop off without showing any development of the ovary, in the same way that they do if pollination is prevented. This suggested that NAA might interfere with pollination either by inhibiting the germination of the pollen grains on the stigma, or by slowing down pollen tube growth to such an extent that the tubes are unable to reach the ovules in time to effect fertilization. In order to investigate this possibility the following experiment was carried out.

Flowering spurs of the variety Crawley Beauty in the late pink-bud stage were placed in vials of water in a warm greenhouse. Emasculated flowers were sprayed with aqueous solutions of NAA at concentrations ranging from 2-100 p.p.m. and five hours later, when quite dry, the stigmas were pollinated with freshly gathered pollen of the cider apple variety Kingston Bitter. After 19 hours the styles were removed, fixed in formalin-acetic-alcohol, and sectioned longitudinally at 40 μ on a freezing microtome for a study of pollen tube growth.

In all the styles both compatible and incompatible pollen tubes were found. The latter could be readily distinguished not only by their limited growth, but also by their characteristically swollen ends. In styles of flowers which had been sprayed with NAA the lengths of both types of pollen tubes were somewhat reduced, but the most marked effect was on the proportion of incompatible tubes (Table VI). Thus the effect of the NAA has here been to convert what is normally a partially compatible pollination into a virtually incompatible one. With 20 p.p.m. NAA, the proportion of incompatible tubes was as high as 70 per cent., and it is considered that this might well account for the marked reduction in fruit set which results from spraying open flowers with NAA of this concentration.

TABLE VI.

Crawley Beauty × Kingston Bitter. Growth of pollen tubes in style 19 hours after pollination in flowers sprayed with various concentrations of NAA.

Concentration of NAA (p.p.m.)	No. of tubes measured	Incompatible tubes		Mean length of tubes (mm.)	
		No.	%	Compatible	Incompatible
0	63	18	29	4·76	1·50
2	118	45	38	4·27	1·36
5	78	32	41	4·19	1·28
10	73	34	47	4·10	1·34
20	57	40	70	4·06	1·25
50	76	65	87	3·45	1·22
100	78	73	94	3·38	1·19

DISCUSSION.

REDUCTION IN CROP.

These experiments confirm those of previous workers who have shown that NAA applied to apples at any time between full bloom and two to four weeks after petal-fall, depending on the variety, will lead to a reduction in the number of fruits matured. They have shown in addition that two quite distinct mechanisms are involved in the use of NAA as a thinning agent.

When applied at blossom time, those flowers which are fully open at the time of spraying fail to develop and, after a delay of two to three weeks, are shed, suggesting that fertilization has not occurred. The fact that NAA applied to the unopened flower buds does not influence fruit set shows that it has no adverse effects on the development of the sexual organs, such has been shown to occur in the tomato (Hemphill, 1949). It seems likely, therefore, that in the apple, the chief effect of NAA at full bloom is to prevent fertilization by interfering with pollen tube growth. Evidence in support of this is provided by experiment 5, in which it was found that NAA sprayed on to open flowers before pollination induced a typical incompatibility reaction between the stylar tissue and the pollen tubes. There is no evidence from these or previous experiments (Luckwill, 1949) that the application of NAA at full bloom increases the physiological drop of developing fruitlets.

Post-blossom applications of NAA, on the other hand, thin the crop by increasing the drop of young fruitlets, and experiment 4 indicates that this increased drop is the direct result of seed abortion induced by the treatment with growth-substance. The exact period after petal-fall during which the seeds are susceptible to damage by NAA was not determined accurately, but it obviously varies rather widely for different varieties of apple. In Crawley Beauty some indication was obtained that the change from the free-nuclear condition to the cellular condition of the endosperm might define the critical limit beyond which NAA is without effect on seed development. Previous work (Luckwill, 1953) has shown that this change is an event of great significance in the development of the apple, since it marks the stage at which the endosperm first starts to produce a natural hormone responsible for the inhibition of fruit drop. Any factor which prevents, or delays cell wall formation in the endosperm, therefore, as petal-fall application of NAA has been shown to do, will lead to an increased abscission of fruitlets during the " first " drop.

In addition to its effect on seed development, NAA itself has a direct inhibiting effect on the development of the abscission layer at the base of the pedicel. This effect, however, is only a temporary one, the duration of which depends on the concentration applied (Barlow, 1950), on the temperature and probably also on the stage of development of the fruit. Throughout these experiments the application of NAA was always followed by a period of from one to three weeks during which no abscission occurred, and it was only after this effect had worn off that the increased drop resulting from NAA-induced seed abortion became evident. When NAA is applied later in the season, e.g. for the control of pre-harvest drop, it has no influence on seed development and the only reaction observed is that of delayed abscission.

INCREASE IN FRUIT SIZE.

Heavy cropping varieties of apple normally respond to fruit thinning by an increase in fruit size. The data from these experiments, however, show that where thinning is carried out with NAA this increase in fruit size may not always occur—in fact, in many instances the fruits on the thinned branches were smaller than those on the unthinned control branches.

Although the reduction in leaf area which occurs in certain varieties following spraying with NAA may contribute to this reduction in fruit size, it is not considered that this is the major factor involved. Reduction in fruit size was most marked on branches sprayed two to three weeks after petal-fall, whereas foliage damage was most severe when the spray was applied at full bloom or petal-fall. Furthermore, the variety Emneth Early, in which the largest reduction in fruit size, was observed, was the one of which the foliage proved most resistant to NAA.

It is concluded, therefore, that NAA has a direct inhibiting effect on fruit growth which tends to offset the advantages gained by thinning and which is more severe the later the spray is applied. In commercial practice this effect could be minimized by using somewhat lower concentrations of NAA (e.g. 15 p.p.m.) and by applying the spray not later than ten days after petal-fall. At this time the initial set can be assessed with some certainty and undue foliage damage can be avoided. It must be stressed, however, that further investigation is needed of the response of individual varieties before the method can be recommended for general use.

BIENNIAL BEARING.

The final assessment of the value of NAA for the control of biennial bearing must await the outcome of more extensive experiments. The failure of any of the thinned branches of Miller's Seedling to flower the following season, however, suggests that these treatments would be ineffective for the control of biennial bearing in this variety. The reason for this may be the marked reduction in leaf area which occurred as a result of spraying with NAA, for, as Singh (1948) has shown, a relatively large leaf area per spur is one of the most important requirements for the differentiation of fruit buds. It is possible that, in other varieties of which the foliage is less sensitive to damage, thinning with NAA might prove more effective in inducing flowering in the " off " year.

SUMMARY.

1. α-naphthalene acetic acid (NAA) in aqueous solution was applied as a spray to branches of three varieties of apple at different times between green-cluster and 41 days after petal-fall. Observations were made on " initial " and " final " set of fruit, fruit drop, fruit weight and foliage damage.

2. The addition of a wetting agent was found to have no influence on the effectiveness of the sprays.

3. Applied at full bloom, NAA (20 p.p.m.) reduced the initial set of fruit but did not increase the subsequent drop. A subsidiary experiment suggested that the reduction in set might be the result of incompatibility between the pollen tubes and the stylar tissue, induced by NAA.

4. Post-blossom applications of NAA (20 and 50 p.p.m.) reduced the " final " set of fruit by increasing the early drop of fruitlets. This heavier drop resulted from seed abortion induced by NAA.

5. Observations on Crawley Beauty suggested that cell wall formation in the endosperm defines the critical limit beyond which NAA is ineffective in increasing fruit drop.

6. In all cases the increased drop, following spraying with NAA, was preceded by a period of one to two weeks during which no abscission occurred.

7. NAA has a direct retarding effect on fruit growth and this tends to offset any increases in fruit size which might result from thinning. This effect is more marked the later the thinning spray is applied.

8. In Miller's Seedling, branches thinned with NAA in the " on " year failed to differentiate fruit buds for the following year. A possible reason for this is the marked reduction in leaf area caused by the sprays on this variety, particularly when applied at full bloom.

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THE ORIGIN AND STRUCTURE OF BRIDGE TISSUES IN RING-GRAFTED APPLE STEMS

By **BARBARA MOSSE**
East Malling Research Station, Kent

THE operation of ring-grafting consists in the removal of a ring of bark from the stem, and its replacement by a similar ring taken from another variety. Garner (1947) has drawn attention to the risk of bridge tissues being formed from the underlying stem, at the point where the two vertical edges of the split ring are brought together.

In the course of experiments to determine whether the introduction of bark rings of clonal dwarfing rootstocks would affect the growth of scions budded on a vigorous rootstock, it was observed that bridge tissues may form in more than one place. The opportunity was therefore taken to examine the anatomy of the tissues involved, and to determine the mode of origin and structure of the bridges.

MATERIAL.

The trees examined consisted of: (1) Cox's Orange Pippin budded on M.XVI rootstock, the stem of the latter having been ring-grafted previously with bark rings derived from the rootstocks 3426, very dwarfing (Tydeman, 1943); M.IX, dwarfing; M.XVI, very vigorous.

(2) Control trees of Cox's Orange Pippin on M.XVI without a ring-graft.

The trees had been raised as follows. Rooted layers of M.XVI were planted in randomized blocks in nursery rows in the autumn of 1944. A ring of bark, one inch wide, was removed from the stem three inches above ground level in the following summer, and replaced by a bark ring of another rootstock. The bark rings were held in position with grafting tape. They did not contain a bud. In July 1945, a month after ring-grafting, the rootstocks were budded with Cox's Orange Pippin, seven inches above ground level.

Nine trees from each treatment were lifted and examined in the spring of 1948, when the scions were two years old and the bark rings had made three seasons' growth. By this time all the bark rings derived from the clonal rootstocks M.IX and 3426 had been split by bridges of the M.XVI rootstock.

RESULTS.

Effect of ring-grafts on growth of the scion.

Tree weight and trunk diameter were recorded as a measure of tree size. The results are given below.

Trees of Cox's Orange Pippin on M.XVI, ring-grafted with:	M.XVI	M.IX	3426	Without ring-graft
Mean weight per tree (lb.)	1·4	1·5	1·6	1·8
Mean diameter of trunk (cm.) measured 5 cm. above bud union	1·75	1·78	1·87	1·94

Figures bracketed together did not differ significantly. P=0·05.

Two conclusions can be drawn from these results.

(1) Differences between trees with M.XVI ring-grafts and control trees without ring-grafts show that a slight check resulted from the operation of ring-grafting, and that this was still apparent two years later.

(2) Differences between trees with M.XVI, M.IX and 3426 ring-grafts were very small, but slightly more growth was made by the trees with 3426 bark rings, the most dwarfing of the three clonal rootstocks.

None of the trees had formed any fruit buds.

The conclusion that the bark rings of clonal dwarfing rootstocks did not reduce the growth or increase the precocity of the Cox's Orange Pippin scions is contrary to that reached by Roberts (1934). However, the establishment of bridges across the dwarfing bark rings may account for the different result.

The origin of bridging tissues.

The bridges of M.XVI tissue had evidently grown strongly, since they comprised more than half the circumference in some of the trees, and had completely altered the shape of the trunk at the point of ring-grafting. Fig. 1 shows diagrams of the cross sections of typical trees when they had been sawn across in the middle of the bark ring. All the M.IX rings had been split, and bridges of stock tissue had become established, generally where the vertical ends of the bark ring had met. Two bridges were formed across most of the 3426 rings, frequently at opposite sides of the stem as shown in Fig. 2. In this photograph the tissues derived from the 3426 bark ring are clearly distinguished from those of the M.XVI bridges by the

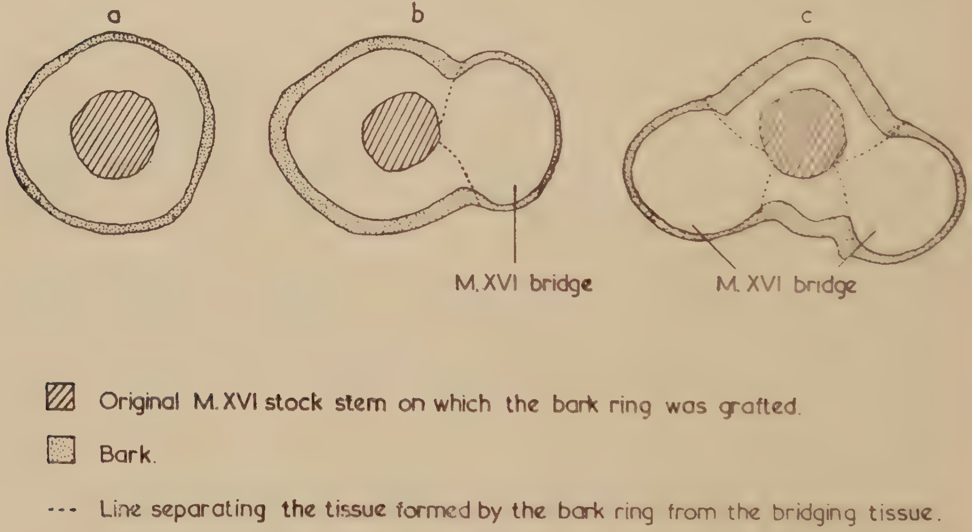
a
b
c
M.XVI bridge
M. XVI bridge
▨ Original M.XVI stock stem on which the bark ring was grafted.
⬚ Bark.
--- Line separating the tissue formed by the bark ring from the bridging tissue.

FIG. 1.

Diagrams of appearance, in cross section, of three-year-old stems of M.XVI ring-grafted with: (*a*) M.XVI, (*b*) M.IX and (*c*) 3426, showing bridges of M.XVI tissue in (*b*) and (*c*).

difference in their colour and in the width of the bark. Differences in the width of bark are shown in greater detail in Fig. 3. There was also a difference in the rate of oxidation, 3426 tissues going brown much more quickly, and in the amount of shrinkage which took place on drying. The right-hand bridge in Fig. 2 shows three seasons' growth, and its annual rings are continuous with those of the ring-graft tissues. The smaller bridge on the left side is only two years old, and it contains no annual ring continuous with that formed in the ring-graft tissue in the year of grafting.

The bridges of M.XVI seemed to have originated in two ways. In some bark rings the ends had apparently never joined, and bridges had arisen directly by proliferation from existing cells of the underlying rootstock. Other bridges, however, had arisen by splitting the overlying bark rings. This must have happened where there was more than one bridge, as in Fig. 2. In such cases the M.XVI bridges had apparently arisen from concentric bundles formed from recently differentiated xylem elements near the outer edge of the underlying rootstock, after the bark rings had made some growth. Fig. 4 shows two such bundles in detail. They consist of small lignified cells, arranged in concentric rows, and resemble the medullary bundles sometimes found in the pith of apple stems. In some bundles, all the cells had become lignified and it seemed unlikely that the bundle could grow any more. In others, a region of meristematic cells remained in the centre and, in some cases, such bundles had reached considerable size (up to 1·14 sq. mm.), and seemed to be still growing. In some places a row of adjoining bundles had coalesced and seemed to be growing outwards through the bark ring tissues as in Fig. 5. The white arrow in Fig. 6*b* shows a large concentric bundle lying above the first season's growth of the bark ring tissues. The arrangement of the tissues just below it and the position of smaller concentric bundles at X suggest that this bundle has grown through the overlying bark ring, and there is a substantial bridge of M.XVI tissue arising from it laterally, Fig. 6*a* and *b*. The bridge is only two years old, and this shows clearly that bridges of stock tissue can penetrate the overlying bark ring after this has become established and made some growth. Other sections suggested that new bridges might arise even later from concentric bundles which had been pushed out farther through the bark ring tissues, but had not yet established a bridge.

The smaller concentric bundles shown at X in Fig. 6*b* are apparently of limited growth. Similar small concentric bundles, consisting entirely of lignified cells, occurred in all the ring-grafted trees, even when the bark ring was derived from the vigorous rootstock M.XVI. But, in this case, all the concentric bundles remained small and none grew out. It seems therefore that the formation of concentric bundles, from which bridges can arise, may be a common sequence to the operation of ring-grafting. In the trees examined, further growth of the bundles only occurred when the bark ring belonged to a more dwarfing type than the underlying rootstock.

The anatomical structure of bridge tissues and of tissues formed from the bark rings.

It was desired to investigate the structure of the bridge tissues and of the adjoining tissues of the bark rings to see how the sharp differences which were observed between the two tissues, and which are illustrated in Fig. 2, might be correlated with their anatomical structure. The two features examined were :

(*a*) the proportion of bark to wood (bark percentage) ;
(*b*) the relative areas occupied by the different elements of the xylem.

Beakbane and Thompson (1947) found that both these characters could be used as diagnostic features to distinguish the roots of the clonal apple rootstocks M.XVI, M.IX and 3426.

Bark percentage. The bark percentage was measured in three trees from each ring-graft treatment. The stem was sawn across transversely at the middle of the bark-ring, the surface planed off, and its image projected on squared paper, at a magnification of ×4, by means of a Vicker's Projection Microscope. The areas occupied by wood and bark respectively were estimated by counting the squares, and the relative amount of bark was expressed as a percentage of the total cross-sectional area. The bark percentage was recorded separately for the M.XVI bridges, and for the tissues derived from the bark rings, which will be called ring tissues. The original M.XVI wood cylinder, shown in Fig. 1, was added to the area of wood of the ring tissues, because it was desired to measure the proportion of bark to wood for each of the clonal types, and the ring of bark used as grafting material had surrounded a core of wood similar in size to that of the original M.XVI wood cylinder.

The ring tissues of M.XVI, M.IX and 3426 differed in their bark percentages as shown :

M.XVI	M.IX	3426	Sig. diff. $P=0{\cdot}05$
15·7	23·0	32·0	5·92

There was no significant difference in the bark percentages of M.XVI tissues, whether occurring as bridges or as complete rings.

The difference in width and structure of the bark of M.IX ring and M.XVI bridge tissues is illustrated in Fig. 3. It can be seen that there are many phloem and pericycle fibres in the bark of the M.XVI bridge, and that the fibres end suddenly where the bridge is joined to the M.IX ring tissue. The same sudden change in bark structure occurred when the ring consisted of 3426 tissue. A lack of phloem and pericycle fibres is characteristic of the stems of the unworked rootstocks M.IX and 3426, while fibres are strongly developed in the stems of M.XVI. The bark percentages of M.XVI, M.IX and 3426 rings also differed in the same way as they do in stems of these three rootstocks when they are allowed to grow unworked.

Wood anatomy. The relative areas occupied by fibres, vessels, rays and parenchyma cells were determined. For the examination of the wood (xylem) a relatively small sample was used (about $\frac{1}{8}$ of the complete cross-section). Transverse sections were cut from the fresh material and were stained in Safranine and Fast Green. Sections were cut from three trees in each treatment. Ring-grafted trees with bridges were sectioned in three positions (Fig. 7) :

i. in the ring tissue ;
ii. in the bridge tissue ;
iii. in the stock stem 1·5 in. above the bark ring.

Trees with M.XVI ring-grafts were sectioned in the ring, (i), and in the rootstock stem above the ring, (iii). In control trees without a ring-graft, sections were made of the rootstock stem at a height comparable with position (iii) Fig. 7. Sections were also cut of stems of the unworked rootstocks M.XVI, M.IX, and 3426 to see how far the anatomical structure of tissues arising from bark rings remained characteristic of their clonal type.

The areas of fibres, vessels, parenchyma and rays were estimated by weighing the corresponding parts cut from photographic prints of the transverse sections, by the method used by Beakbane (1941).

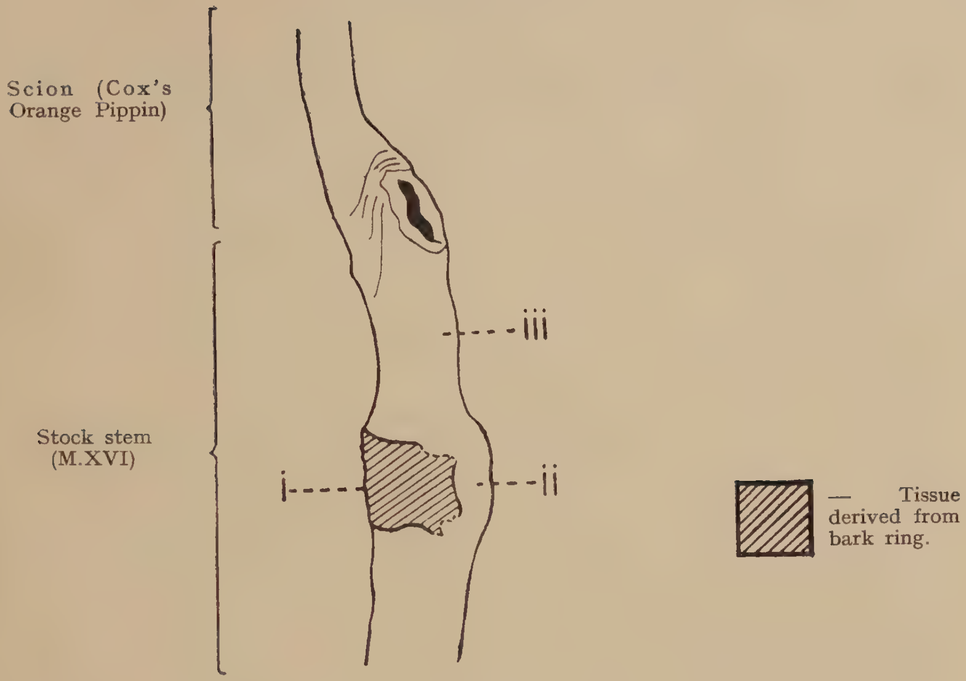

FIG. 7.

Diagram of part of a ring-grafted tree with a bridge of stock tissue, to show the positions selected for sectioning.

The photographs were taken at the middle of the last annual ring, i.e. the ring formed in 1947, one photograph being made from each section, at a place where the structure was considered to be typical of the section. A more elaborate method of sampling was not employed, since the aim of the investigation was only to give a general survey of the structure. The results are shown in Table I, which gives the comparison within trees of M.XVI stem, M.XVI bridge and 3426 or M.IX ring tissue.

It is evident that the tissues formed from the dwarfing bark rings M.IX and 3426 differed considerably from those of the M.XVI bridges and of the M.XVI rootstock stem above the bark ring, in the relative proportions of the different elements of the wood. They also differed from M.XVI tissues in the shape and distribution of the cells. This point can be seen by comparing Figs. 8 and 9.

Comparison of the unworked rootstock stems of M.XVI, M.IX and 3426, which are illustrated in Fig. 8*b*, *d* and Fig. 9*d*, showed that the shape, arrangement and relative area of the wood elements were different for each clonal type. The tissues derived from the dwarfing bark rings were very similar to those of the unworked rootstocks of the same clonal type as is shown in Fig. 8*a* to *d*. This result differs from that of Roberts (1934), who states that " the new xylem formed under the ring was like the ring variety, like the stem variety, or in some cases resembling neither ". It has been observed by Yeager (1944) and others, that bark rings of purple sapped varieties give rise to purple sapped wood beneath them, and this observation supports the present findings that the anatomical structure of tissues formed from bark rings

TABLE I.

Relative areas of rays, parenchyma, fibres and vessels in the wood of bridge tissues, bark ring tissues and of the rootstock stem above the bark ring.

Type of tissue :— Position :—	M.IX ring (i)	M.XVI bridge (ii)	M.XVI stem (iii)	Sig. diff. $P=0\cdot05$
Fibres	37	63	65	7·4
Rays	39	19	22	5·8
Parenchyma	13	4	2	3·4
Living tissue (rays and parenchyma)	52	23	24	5·8
Vessels	11	14	11	3·3
	3426 ring (i)	M.XVI bridge (ii)	M.XVI stem (iii)	
Fibres	40	59	64	11·6
Rays	40	24	20	16·0
Parenchyma	10	3	3	8·2
Living tissue (rays and parenchyma)	50	27	23	13·7
Vessels	10	14	13	3·3

Note.—The relative areas of the different elements are expressed as a percentage of the wood.

resembles very closely that of the plant from which the ring is derived. It is worth noting that the only feature in which M.XVI, M.IX and 3426 tissues in the ring-grafted trees resembled each other was their vessel area, which varied only from 10 to 14 per cent. This will be discussed later.

All the M.XVI tissues, whether occurring as bridges, as complete bark rings, as stems above bark rings or in control trees without a ring-graft, were very similar. With the exception of vessels which occupied a slightly larger area in control trees, there were no significant differences ($P=0\cdot05$) in the percentage areas of rays, parenchyma, fibres, vessels and living tissue between any of the M.XVI tissues.

Stems of unworked M.XVI rootstocks from three different sources were used as a comparison. There was no significant difference ($P=0\cdot05$), in the percentage areas of vessels and rays in stems from the three sources, indicating that they represented adequately the structure of the unworked M.XVI rootstock stem. This differed significantly ($P=0\cdot001$) from the same rootstock under Cox's Orange Pippin scions in areas of rays and vessels. The figures in Table II show that the vessel area was twice as large and the ray area approximately half as large in stems of the unworked rootstock.

Fig. 9*a* to *d* illustrates the difference in the relative areas of rays and vessels, and also shows that, apart from this, the Cox's Orange Pippin scions had little effect on the shape and arrangement of the wood elements.

TABLE II.

Relative areas of vessels and rays in stems of the rootstock M.XVI, unworked, and budded with Cox's Orange Pippin scions.

Source	Percentage area of vessels	Percentage area of rays
From unworked stocks	28	12
From trees with Cox's Orange Pippin scions, with and without ring-grafts in the stock stem	14	20

DISCUSSION.

It is evident that the tissues examined in the ring-grafted trees had undergone little alteration as a result of their proximity to other genetically distinct tissues. They retained the characteristic anatomical structure of their clonal variety when they consisted only of a ring of tissue between two different clonal varieties and also when they arose in unusual ways like the bridging tissues.

It is believed that the origin of bridging tissues from concentric bundles, formed near the outer edge of the underlying rootstock stem, has not been previously described in apples. This observation has a bearing on the practice of ring-grafting. Concentric bundles of small size were found in all the ring-grafted trees, irrespective of whether the bark ring belonged to a dwarfing or a vigorous type of rootstock. It seems probable that something in the operation of ring-grafting, perhaps the removal of a ring of bark, may encourage the formation of concentric bundles. If this is so, then there is a risk that bridges might arise from such bundles over a period of years, even when the operation of ring-grafting has been performed in two stages as described by Garner (1947). In the present trial the risk of bridging was greatest with bark rings of the most dwarfing rootstock. Since it seems impossible to ensure in practice that a ring-graft shall remain unbroken, it is doubtful whether ring-grafting with a one-inch-wide bark ring is a suitable method for testing either new rootstocks or intermediates as has been suggested elsewhere.

The fact that the M.XVI tissues developed under the Cox's Orange Pippin scion differed markedly from tissues of the same rootstock unworked whether or not a ring of other tissue had been inserted, requires an explanation. It is suggested that the reduction in vessel area and increase in ray area were an effect of the Cox's Orange Pippin scion, and that the total vessel area in the stems of grafted trees may be partly determined by the leaf-bearing scion. This view is supported by the small variation in vessel area of the three clonal varieties of which the ring-grafted trees were composed, and also by some observations of White (unpublished) and of Salisbury (1913) on the correlation between lamina size and vessel area of petioles.

Further work is in progress to investigate this point more fully, as it would have a bearing on stock/scion relationships.

SUMMARY.

Bark-rings of M.XVI, M.IX and 3426 were grafted into the stems of M.XVI rootstocks budded with Cox's Orange Pippin scions. All bark rings of the dwarfing

clonal rootstocks 3426 and M.IX had become bridged after three seasons' growth, sometimes in several places. They had not affected the growth or precocity of the scion.

A study was made of the origin and anatomical structure of the bridging tissues, and of the structure of tissues derived from the bark rings.

The origin of M.XVI bridges from concentric bundles, formed after ring-grafting, near the outer edge of the rootstock stem beneath the bark ring, is described, and its bearing on the practice of ring-grafting is discussed.

Bridge tissues of M.XVI were very similar in their wood and bark structure, and in the proportion of bark to wood, to tissues derived from M.XVI bark rings, to M.XVI stems above bark rings, and to M.XVI stems under Cox's Orange Pippin which had not been ring-grafted and were used as controls. They differed markedly in the relative areas of vessels and rays from stems of the unworked rootstock M.XVI and this is attributed to the presence of the leaf-bearing Cox's Orange Pippin scion in ring-grafted and control trees.

Tissues derived from bark rings of the dwarfing rootstocks M.IX and 3426 differed strikingly from the surrounding tissues of M.XVI in the structure and in the relative proportions of wood and bark. They were similar in anatomical structure to stems of the same rootstocks unworked.

ACKNOWLEDGMENTS.

Thanks are due to Mr. R. J. Garner for putting the trees at the disposal of the author ; to Dr. A. B. Beakbane for much help and advice during the investigation and in the presentation of the paper ; to Mr. J. Taylor for undertaking the statistical analysis, and to Miss E. C. Thompson for the photographs.

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PLATE I.

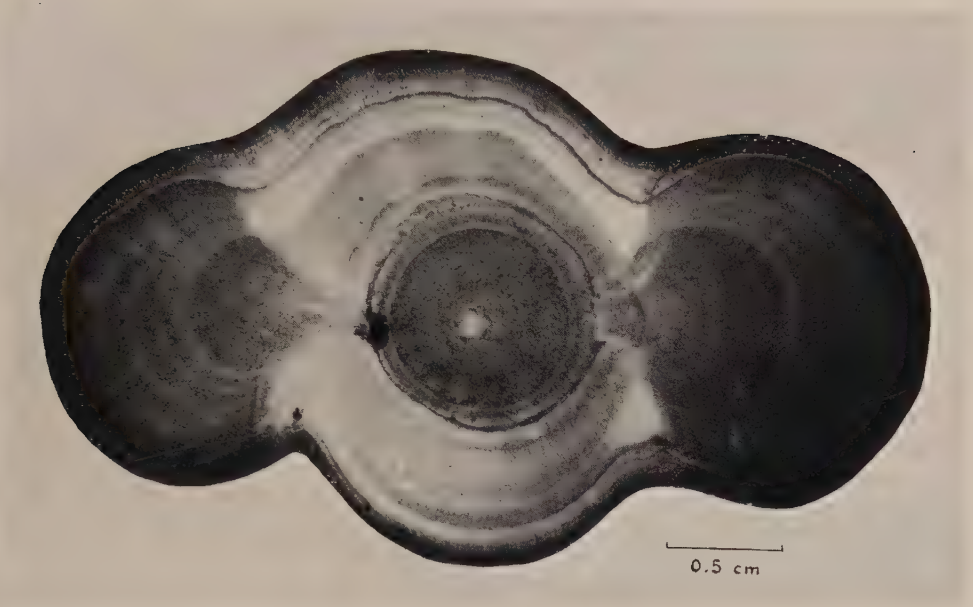


FIG. 2.

Appearance, in cross section, of M.XVI bridge and 3426 ring tissues, three years after the stem had been ring-grafted with 3426.

Note the splitting of the bark ring tissue and the development of two large bridges of M.XVI on either side of the stem. The bark ring tissue appears pale, and the M.XVI tissue dark, owing to differences in their structure.

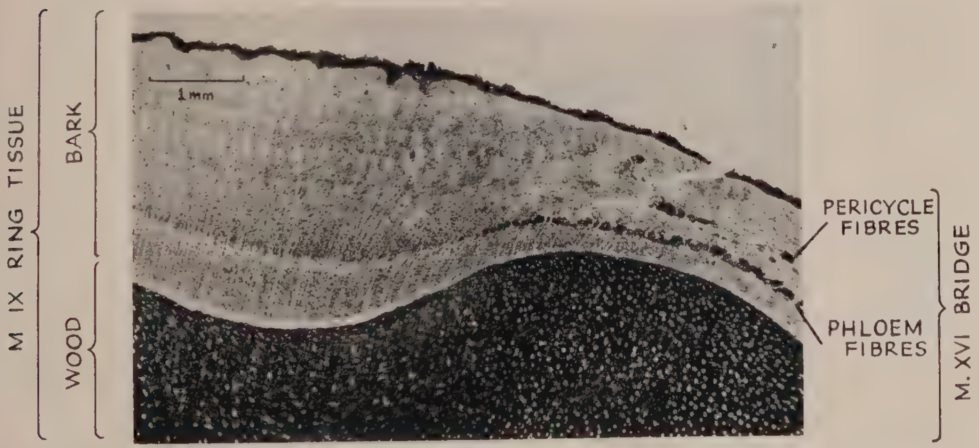

1mm
M IX RING TISSUE
BARK
WOOD
PERICYCLE FIBRES
PHLOEM FIBRES
M.XVI BRIDGE

FIG. 3.

Transverse section through a bridged ring-graft of M.IX, showing differences in the bark structure of ring and bridging tissues.

PLATE II.

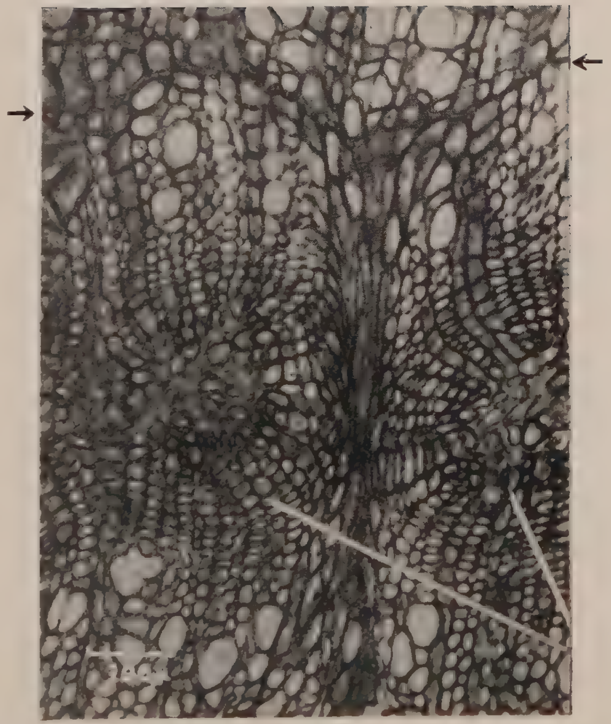


Fig. 4.

Transverse section of concentric bundles (indicated by white pointers), formed, after ring grafting, near the outer edge of the M.XVI wood cylinder.

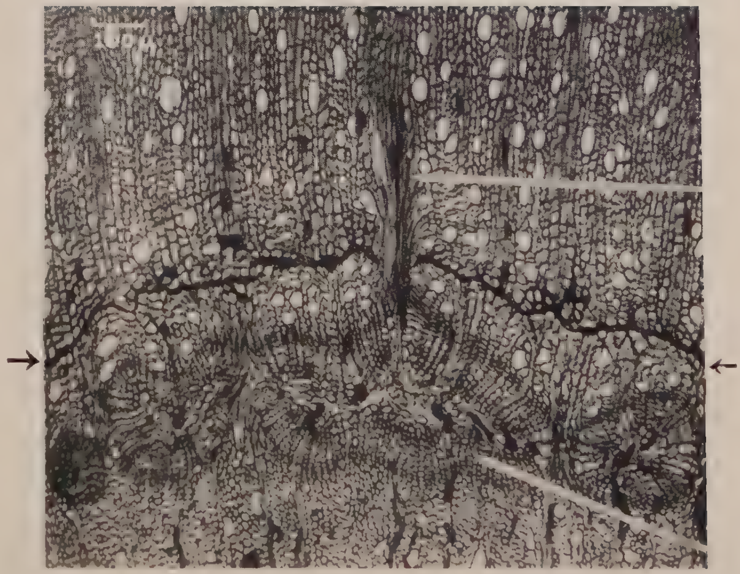


Fig. 5.

Transverse section of coalescing concentric bundles formed in M.XVI stock stem underneath M.IX bark ring tissues.
Note the extension of the M.XVI tissues from a concentric bundle into the bark ring.

Black arrows in Figs. 4 and 5 indicate a line of disintegrating cells, injured in the grafting operation, and separating the ring tissues (above) from the underlying woody tissue of the rootstock stem (below).

PLATE III.

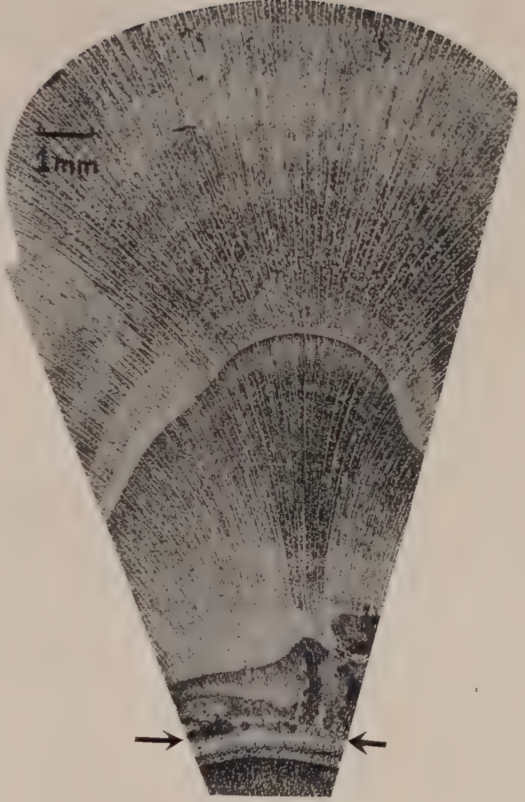


FIG. 6 (*a*).

Transverse section of two-year-old M.XVI bridge across a ring-graft of M.IX showing three seasons' growth. Black arrows indicate junction of ring tissue (above) with rootstock stem (below).

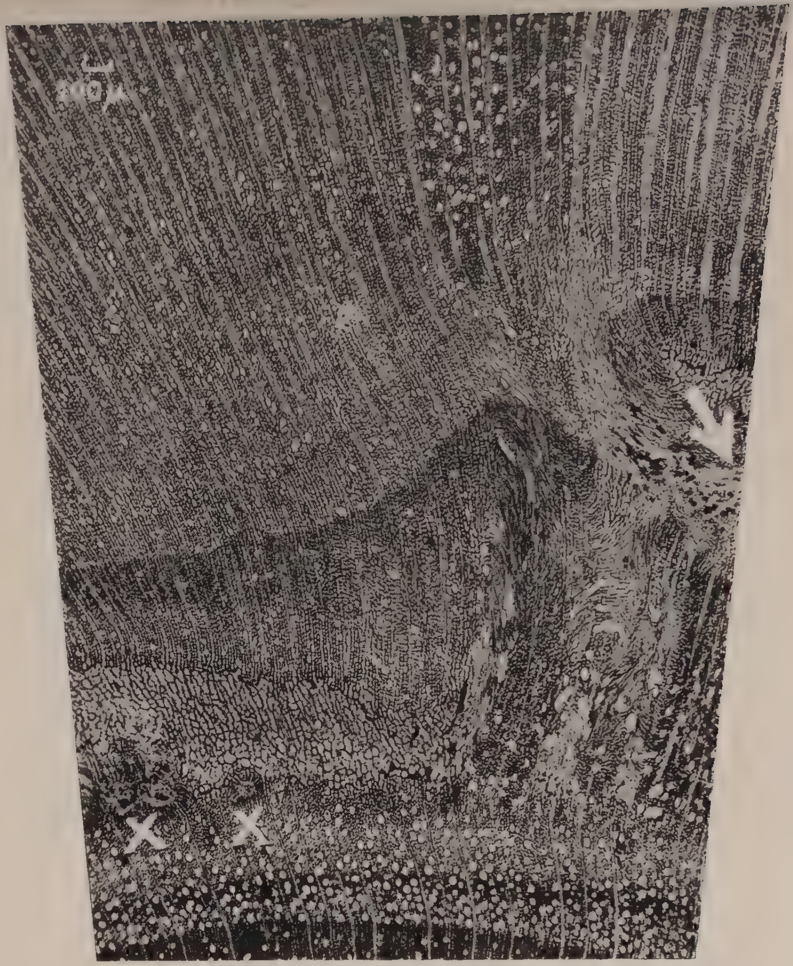


FIG. 6 (*b*).

Detail of lower half of Fig. 6 (*a*). Note concentric bundles of limited growth above X; concentric bundle which has given rise to M.XVI bridge is indicated by the white arrow.

PLATE IV.

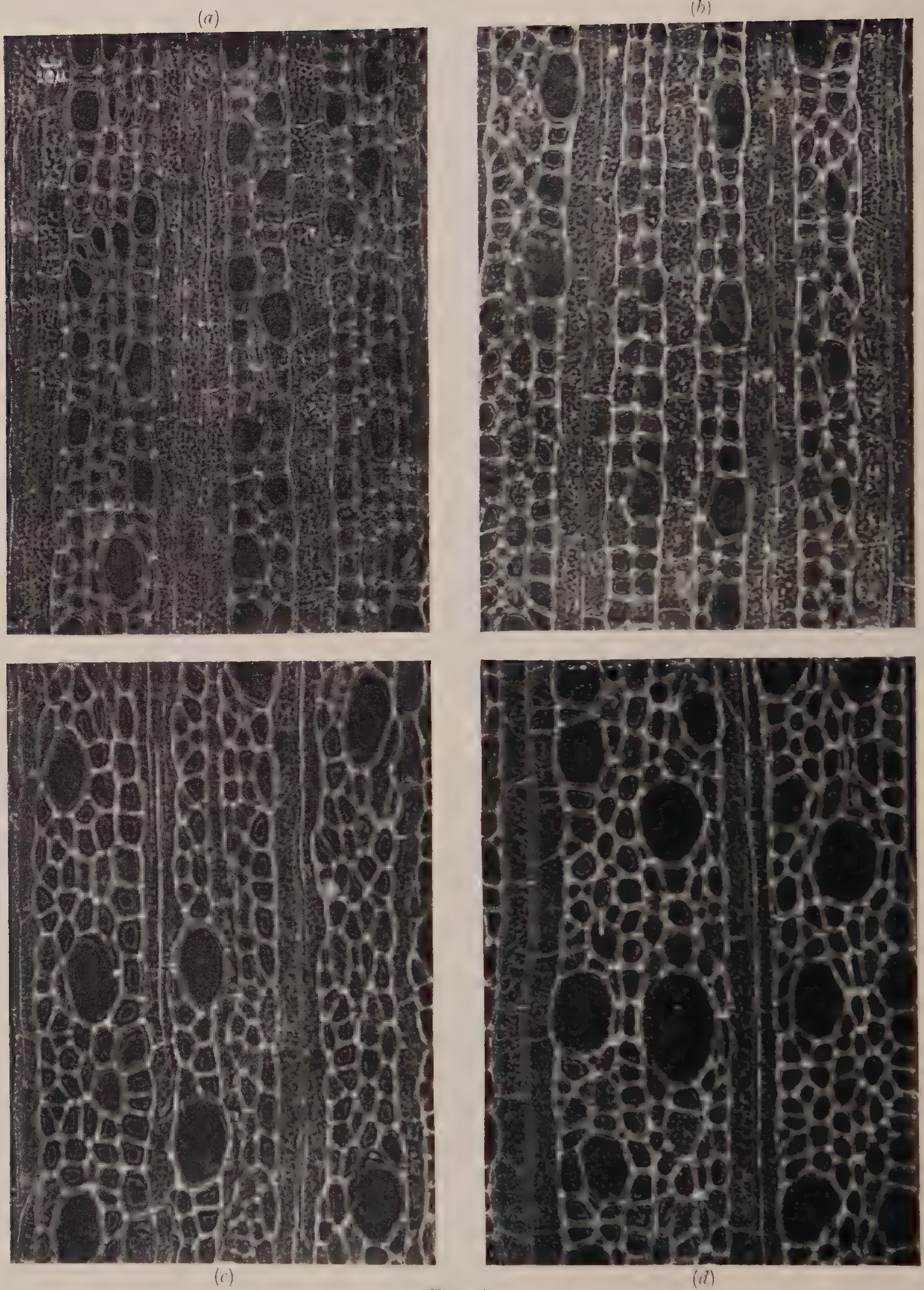


Fig. 8.

Transverse sections of the wood in stems of the apple rootstocks 3426 (*a*) (*b*), and M.IX (*c*) (*d*). (*a*) and (*c*) derived from bark rings inserted into the rootstock stem of M.XVI budded with Cox's Orange Pippin.
(*b*) and (*d*) from the unworked rootstocks.

PLATE V.

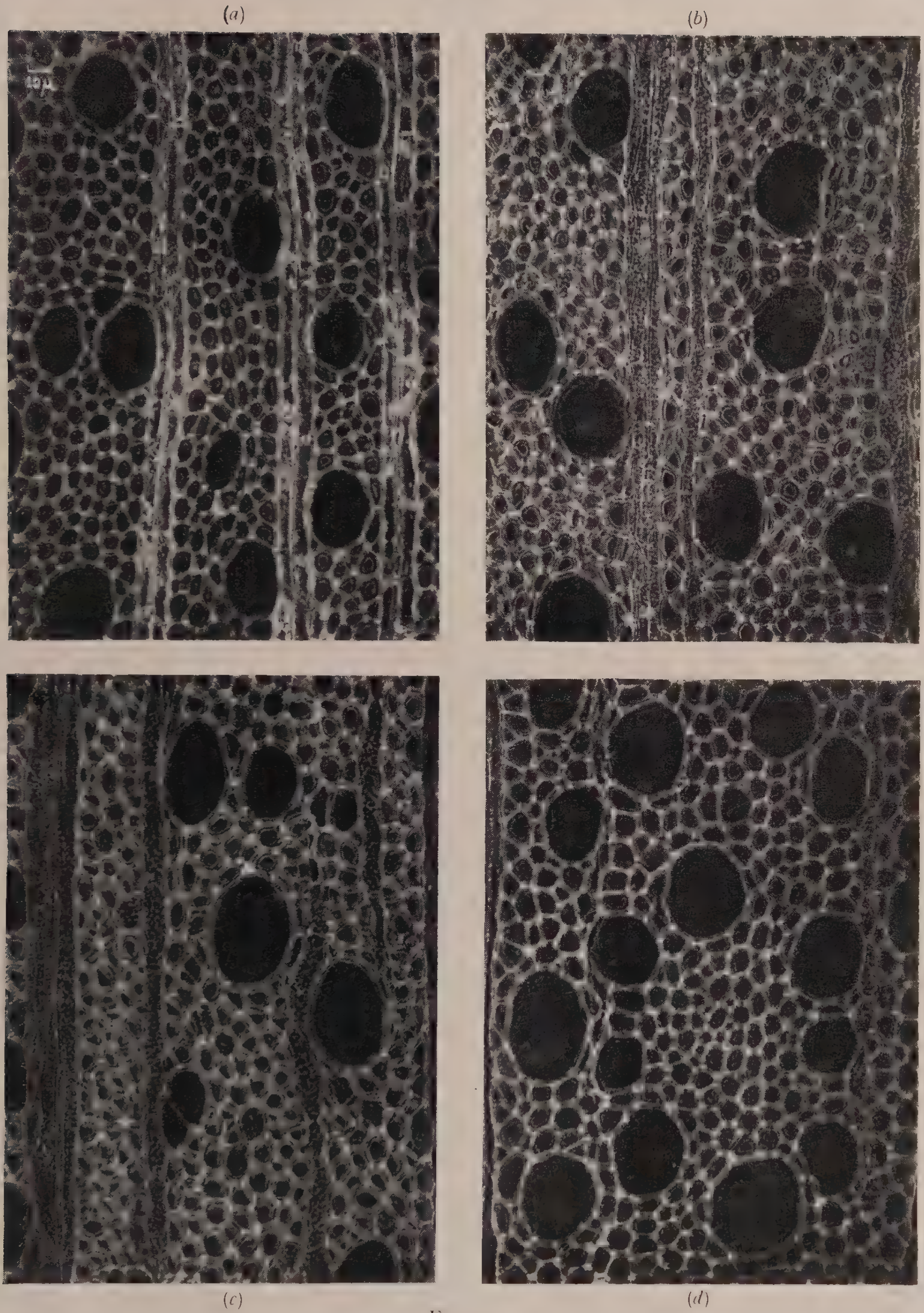


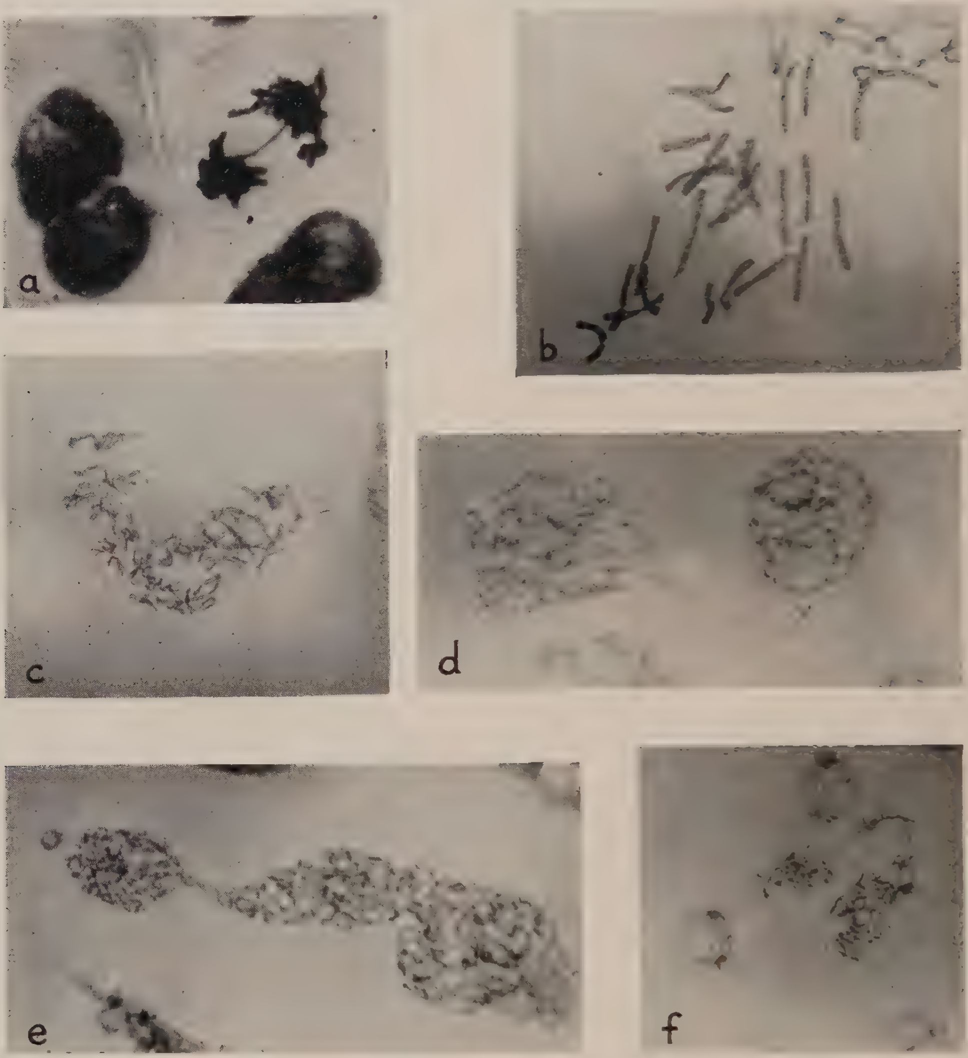
FIG. 9.

Transverse sections of the wood in stems of the apple rootstock M.XVI.

(*a*) from a tree budded with Cox's Orange Pippin.
(*b*) derived from a bark ring inserted into the rootstock stem of M.XVI budded with Cox's Orange Pippin.
(*c*) from a bridge of M.XVI across a 3426 bark ring.
(*d*) from the unworked rootstock.

THE EFFECT OF HEXACHLOROCYCLOHEXANE ON MITOSIS IN ROOTS OF THE ONION (*Allium cepa*) AND STRAWBERRY (*Fragaria vesca*).
BY MARY E. SCHOLES.

PLATE I.



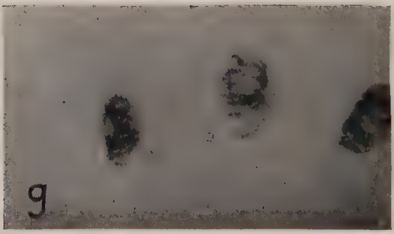


FIG. 4.

Microphotographs of treated root-tips of *Allium cepa*.
PETRI DISH MATERIAL. **0·03 gm. flea beetle dust**:—(*a*) Laggards in telophase and bi-nucleate cell. (×720.) (*b*) Polyploid scattered metaphase showing stickiness between chromosomes. (×720.) (*c*) Polyploid metaphase showing the effect of spindle inhibition. (×495.) **0·03 gm. gamma isomer on gypsum**:—(*d*) Prophases joined by a bridge persisting from previous anaphase. (×720.) **0·06 gm. gamma isomer on gypsum**:—(*e*) Prophase with detached portion arising from large, irregular interphase nucleus. (×720.) (*f*) Complex anaphase involving three cells joined together, but affected differently. (×495.)
POT MATERIAL. **0·12 gm. flea beetle dust**:—(*g*) Telophase with two exclusions. (×720.)

THE EFFECT OF HEXACHLOROCYCLOHEXANE ON MITOSIS IN ROOTS OF THE ONION *(ALLIUM CEPA)* AND STRAWBERRY *(FRAGARIA VESCA)*

By **MARY E. SCHOLES**
Elsenham, Bishop's Stortford, Herts.

SYNOPSIS.

Experiments were carried out with a proprietary flea beetle dust containing crude BHC to ascertain whether, employed as an insecticide, it has any effect on cell division. Root-tips of onion seedlings and strawberry runners were used as test material and the doses were equivalent to 40-200 pounds per acre of flea beetle dust. By germinating onion seeds in direct contact with the insecticide it was shown that it has two effects on the chromosomes. The frequency of nuclear divisions was unaffected, but low doses may lead to the exclusion of nuclear fragments in subsequent cell divisions and higher doses may lead to polyploidy. Both effects were produced by the dust and the gamma and delta forms of BHC when used separately. The alpha and beta forms were only slightly active in high concentrations. The milder effect was particularly evident for a period of at least four days after removal from the insecticide.

In a series of pot experiments it was shown that relatively high doses had only a slight effect on cell division, but there is a definite risk of causing genetic changes. There is also a risk that the insecticide may cause the death of some cells, or even roots, where local concentrations are high ; to spread evenly the minimum dose necessary for insect control is, therefore, important.

The hazards which may be involved in the widespread use of BHC as an insecticide are discussed. It is clear that the effects on the chromosomes may lead to genetic changes in the affected plants or their progeny although these plants may appear to be unaffected. This is important in seed production or in growing plants in which the constitution of the progeny should remain unaltered. The use of fruit tree sprays containing BHC should also be carefully considered where young wood is used for scions in grafting.

INTRODUCTION.

The insecticidal action of crude hexachlorocyclohexane is due almost entirely to the presence of the gamma isomer (Slade, 1945). The extensive literature on the uses of this insecticide has been reviewed by West and Campbell (1950). Jameson, Thomas and Woodward (1947) reported marked increases in yields of oats and wheat, with marked decreases in wireworm population, on land treated with the insecticide. It was assumed that it had no deleterious effect on the plants. There are now numerous published references to the phytotoxicity of hexachlorocyclohexane, viz. McLeod (1946), Smith (1948), Stoker (1948), Hocking (1950), Ashby (1950) and many others.

Nybom and Knutsson (1947), investigated the cytological effects of hexachlorocyclohexane on roots of *Allium cepa* and found that the gamma isomer and the crude material produced polyploidy, the alpha isomer produced partial polyploidy, while the beta isomer was entirely without such an effect. Kostoff (1948, 1948*a*, 1949), working mainly with cereals, found that the gamma isomer produced thickening of the root-tips and coleoptiles and that the affected tissues showed polyploidy and other cytological abnormalities. Östergren and Levan (1943) had previously produced polyploidy in *Allium cepa* with bromocyclohexane and partial polyploidy with cyclohexane. Carpentier and Fromageot (1950) found that both the gamma and delta isomers produced polyploidy, but the delta isomer had an independent toxic effect as the concentration was increased.

Smith (1948) investigated the persistence of hexachlorocyclohexane in acid and alkaline soils kept in the open and was able to recover 80 per cent. of the original content after 18 months. A rough estimate of the rate of decay from this figure suggests that 50 per cent. of the original application may be found in the soil 4½ to 5 years later. On account of its low solubility in water, little would be leached out and it seems reasonable to suppose that it would repeatedly be brought near the surface and in contact with the roots of each succeeding crop. Martin (1950) also considered the disadvantages of great chemical stability in compounds used as insecticides.

It was, therefore, thought to be of practical importance to ascertain whether doses normally used in agriculture are likely to cause polyploidy or other cytological abnormalities which might adversely affect the treated and any future generations, and whether it would be practicable to use the gamma isomer to produce polyploids.

THE INSECTICIDES.

The insecticides used in these experiments were (*a*), a proprietary flea beetle dust containing about 2 per cent. crude hexachlorocyclohexane, and (*b*), mixtures of each of the isomers, alpha, beta, gamma and delta, with finely ground gypsum to contain approximately the same percentage of each isomer separately as is contained in the flea beetle dust. The samples of the pure, finely ground isomers were mixed with the appropriate quantities of gypsum, were put into glass jars which were only half filled and were turned over and over in a " butter churn " for thirty minutes. The cytological effects on onion seedlings germinated in contact with very small doses of these mixtures left little doubt as to their homogeneity. Seedlings grown in contact with gypsum only were entirely unaffected cytologically.

CALCULATION OF DOSES.

The recommended application of flea beetle dust for the control of that insect is at the rate of approximately 80 pounds per acre, with further applications to combat renewed attacks. The doses used in the field may, therefore, be up to two or three times this figure, and the effective dosage rates will depend on the method of application. It may be applied as a seed dressing, combine drilled or broadcast. Recently Jameson (1950) has described seed treatment with liquid dressings and sowing a mixture of seed and granules of the insecticide. Table I shows the doses used in the present investigation. They were chosen to cover the possible range used in the field and were applied in different ways.

TABLE I.

Range of doses of insecticides used.

gm./pot. (Surface area 0·008 sq. yds.)	oz./acre pure gamma isomer (approx.)	lb./acre crude hexa-chlorocyclo-hexane	lb./acre gamma isomer on gypsum, or flea beetle dust
0·03	1·7	0·8	40
0·06	3·4	1·6	80
0·09	5·1	2·4	120
0·12	6·8	3·2	160
0·15	8·5	4·0	200

PETRI DISH EXPERIMENTS.

A preliminary series of experiments was carried out in Petri dishes to ascertain whether the insecticides had any effects on seedlings germinated in direct contact with them. The flea beetle dust and each of the isomers, alpha, beta, gamma and delta, separately mixed with gypsum, were used. The surface area of the base of a Petri dish compares with the surface area of soil in the pots used in the soil experiments. Twenty-four seeds of the onion, *Allium cepa* var. Ailsa Craig, were used in each experiment. The seeds were washed, placed in the Petri dish between two sheets of filter paper moistened with distilled water and were kept in the dark. The dose of insecticide under investigation was spread evenly on the bottom filter paper. The temperature was not controlled but was recorded with a maximum and minimum thermometer, which indicated a variation between 56° F. and 76° F.

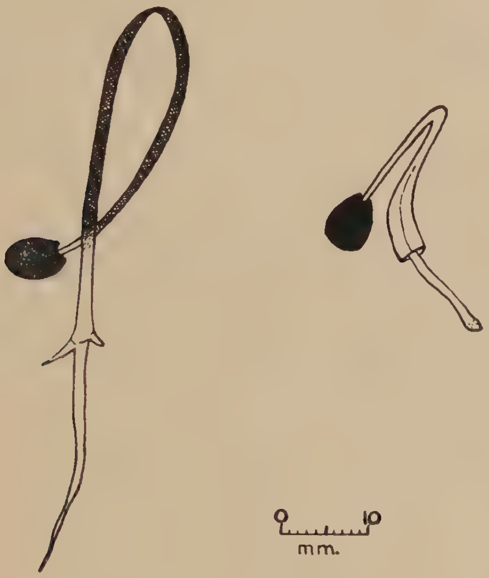


FIG. 1.
Onion seedlings ten days after germination in Petri dishes. Left—Control. Right—Grown with 0·09 gm. gamma isomer on gypsum.

In the control experiments the roots attained a length of 1 cm. in approximately 48 hours after germination. This was taken as the standard of normal growth and root-tips were fixed at this stage. Seedlings from the dressed seed and those grown with doses which were later found to be without cytological effect, attained the normal standard. The doses which caused partial polyploidy reduced the growth rate and all the doses which caused complete polyploidy produced the typical hypertrophy characteristic of the colchicine effect (Dermen, 1940) and shown in Fig. 1. When removed from the insecticide and thoroughly washed, these affected seedlings made no further growth.

CYTOLOGICAL TECHNIQUE.

The root-tips were fixed in acetic-alcohol; they were stained in leuco basic fuchsin after hydrolysis and were squashed, dehydrated and mounted in Euparal.

MITOTIC INDEX AND MITOTIC FORMULA IN PETRI DISH EXPERIMENTS.

The mitotic index is the percentage of cells in a meristem in stages of division from prophase to telophase. To determine this index with any degree of accuracy, Deysson (1948) has shown, in the case of onion roots, that 1,500 to 3,000 cells must be counted. The mitotic formula is the percentage of dividing cells in each of the four phases of mitosis. To determine this formula with accuracy about 400 division figures, which is the greater part of the divisions in each meristem, must be counted. In the onion, the mitotic formula is independent of the length of the root, but the mitotic index varies with the length of the root, being constant for roots of the same length (Deysson).

The mitotic index and mitotic formula were determined for six control roots, each 1 cm. long, by counting 2,500 to 3,500 cells in each root. The results are shown in the first line of Table II.

TABLE II.

Comparison of mitotic index and mitotic formula for controls and treated roots.

Dose in gm.	Mean % dividing cells	Mean % prophases	Mean % metaphases	Mean % anaphases	Mean % telophases
Controls	14·5	41·5	11·9	4·4	42·2
Standard error of control mean	0·55	0·31	0·67	0·43	0·77
0·03 γ isomer on gypsum	13·8	43·1	17·9	4·2	34·7
0·06 ,, ,, ,,	15·7	48·9	28·1	8·1	15·0
0·09 ,, ,, ,,	17·8	43·3	29·8	6·4	20·7
0·03 flea beetle dust ..	14·9	42·2	26·3	11·7	19·9
0·06 ,, ,, ,, ..	14·9	40·1	29·0	9·9	21·0
Sig. diff. (P=0·05) ..	3·02	5·90	7·30	3·50	7·65
Sig. diff. from controls (P=0·05)	2·42	4·18	5·29	2·60	5·55

The standard errors of the control means have been quoted to indicate the degree of accuracy with which these observations can be carried out in control material. It would be fallacious to calculate a significant difference from them. Two significant differences are quoted in each column because the variation between replicates was smaller for controls than for treated roots. A pair of treatments differ significantly if the difference between their means is greater than the first significant difference given. A treatment differs significantly from the controls if the difference between its mean and the control mean is greater than the second significant difference given.

CYTOLOGICAL EFFECTS OF THE FLEA BEETLE DUST AND THE GAMMA ISOMER.

(*a*) *General effects.*

It will be seen (Table II) that there is no appreciable lowering of the mitotic index, although the variance is greater. Its significant increase in the material treated with 0·09 gm. gamma isomer on gypsum may be due to the clumped appearance of some figures recorded as prophase and metaphase. They may remain in this state for some time and add to the total count, or the normal cells may spend a longer time in metaphase and therefore increase the total time spent in mitosis. The most obvious effect is to change the frequencies of the metaphases and telophases, as shown in Table II and Figs. 2 and 3. In this connection it must be pointed out that only two roots in the material treated with 0·03 gm. gamma isomer on gypsum had an abnormal mitotic formula and the points on the graphs have been plotted by taking an average value from these two roots, whereas all other points are derived from an average value from six roots. The other roots in that group were not completely unaffected and reference will be made to them later. Material treated with higher doses was examined, but there was no evidence that increasing the dose had any marked effect.

(*b*) *Effects on the chromosomes.*

The pure gamma isomer has two apparent effects. With the lowest dose investigated there were " sticky " telophase bridges significantly in excess of the number found in control material. In the controls only one bridge was found in 1,144 telophases, whereas seven bridges were found in 649 telophases in three experimental roots. In the fourth root, 60 per cent. of the telophases had bridges

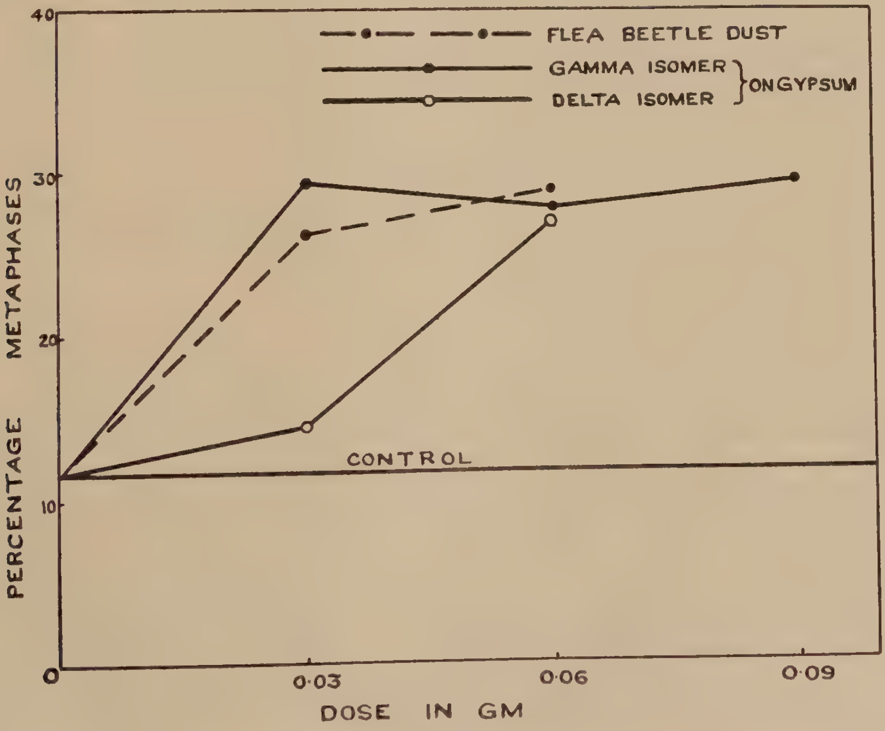


FIG. 2.

Graph showing the frequencies of cells at metaphase after treatment with flea beetle dust and the gamma and delta isomers of hexachlorocyclohexane.

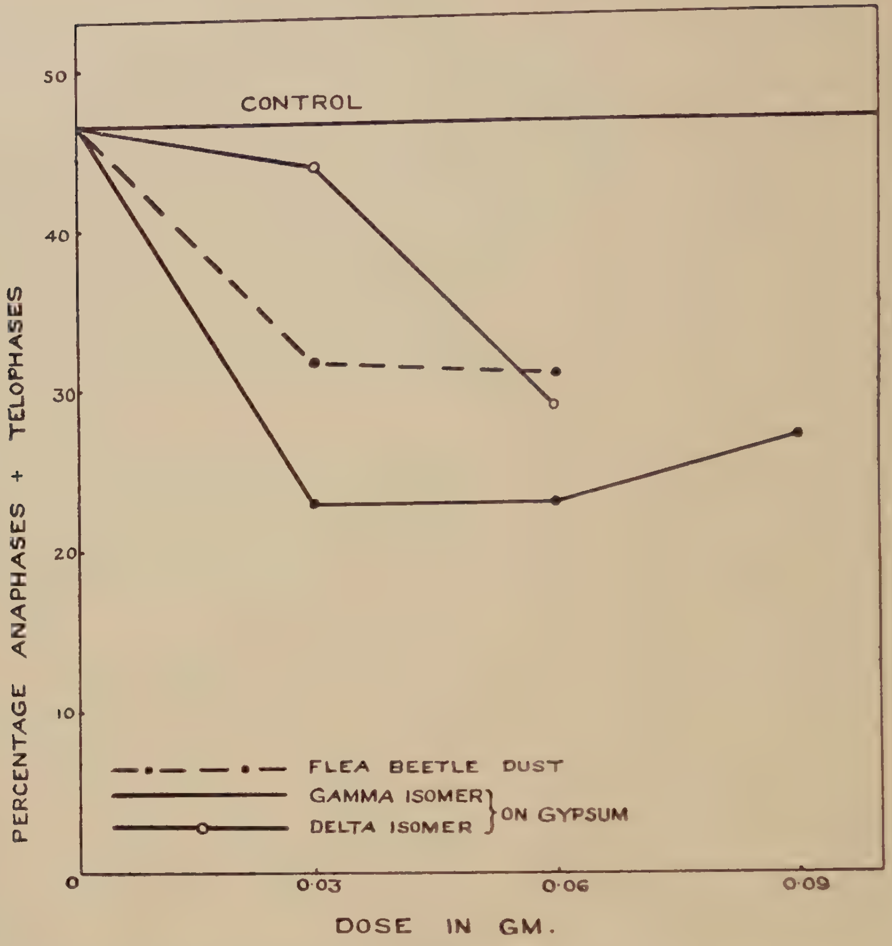


Fig. 3.

Graph showing the frequencies of cells at anaphase and telophase after treatment with flea beetle dust and with the gamma and delta isomers of hexachlorocyclohexane.

(Plate I, Fig. 4*a*). These bridges may, therefore, be regarded as one of the first stages in the action of the gamma isomer. They are usually formed by one chromosome, but occasionally two or more chromosomes are involved. The resting cells are often joined in pairs and this condition may persist into the next prophase, for example, in one root about 50 per cent. of the prophases were double (Plate I, Fig. 4*d*). These bridges may be an important factor in producing polyploidy with a low dose. They are sometimes broken by the laying down of the cell wall and fragments excluded in the separation of the paired nuclei, but in some cells the wall is suppressed and bi-nucleate cells are formed. In other cases small extrusions are cut off from the nucleus. A prophase with a detached portion, which has arisen from a large irregular nucleus, is shown in Plate I, Fig. 4*e*.

The second effect is prevention of spindle formation (Plate I, Fig. 4*c*). With the lowest dose, this effect was evident in only two roots. With the higher doses a large proportion of the cells in all roots are polyploid and, with the exception of a few normal prophases, all the division figures are abnormal. No simple telophase bridges were found, but there is often a " stickiness " between either chromosomes or sister chromatids in late prophase and metaphase (Plate I, Fig. 4*b*). Figures showing a variety of adhesions were found (Plate I, Fig. 4*f*), and these may account for cases of aneuploidy.

The same effects are shown with the flea beetle dust, but polyploidy is produced with the low dose. Presumably " stickiness " would occur with lower doses which are below the normal doses used in agriculture, but which would be realized in treated soil.

POT EXPERIMENTS.

The soil used in these experiments was John Innes Sowing Mixture of the following composition :

Parts by volume : 2 parts loam (partially sterilized by steaming at 180° F.).
1 part peat.
1 part very coarse sand.

To each bushel of this mixture 1½ oz. superphosphate and ¾ oz. ground chalk were added. The pots were watered with rain water collected from a tiled roof and stored in galvanized butts. Twenty-four seeds were sown in each pot. In one set of experiments the insecticide was sown with the seeds, and then covered with ⅛ in. of soil to compare with combine drilling in the field; in the other set of experiments the seeds were sown and the insecticide spread on the surface layer of soil to compare with broadcasting in the field. The doses used are shown in Table III. Lower doses

TABLE III.

Proportion of abnormal seedlings in pot-grown material.

Treatment	Dose gm./pot	No. of seeds germinated per pot in 8 days	No. of abnormal seedlings
Controls	—	16	—
Controls	—	12	—
Gamma isomer on gypsum ; combine drilled	0·15	10	—
	0·15	16	2
Flea beetle dust ; combine drilled	0·09	14	1
	0·12	16	—
	0·12	16	2
	0·15	13	—
Gamma isomer on gypsum ; broadcast	0·15	15	2
	0·15	13	—
	0·15	13	—
Flea beetle dust ; broadcast	0·12	14	—
	0·15	13	—
	0·15	7	—
	0·15	14	2

were not included as it became obvious that fairly heavy doses could be used in soil giving a very high proportion of normal seedlings although, as will be shown later, they do show some cytological abnormalities. Seedlings were raised eight days after sowing and tips from roots of varying lengths were fixed and examined cytologically. The temperature during these experiments varied between 60° F. and 80° F.

The proportion of seedlings with abnormal root development is very low indeed (Table III); they are illustrated in Fig. 5. In studying the treated material, these abnormal roots and six roots of normal development but of varying lengths, from five pots, were chosen. The dose and method of application of the insecticide to each pot are shown in Table IV.

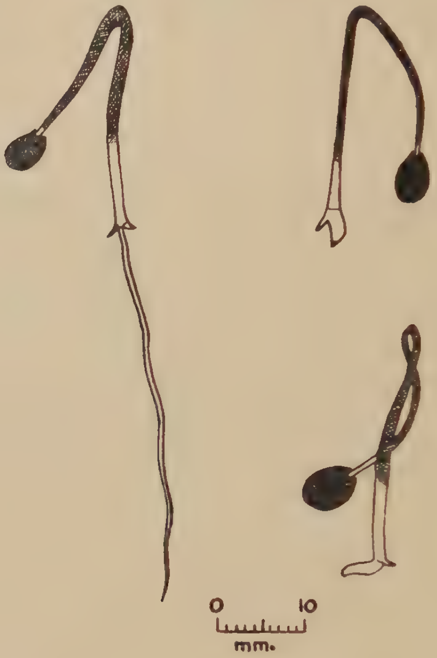


FIG. 5.
Onion seedlings ten days after sowing in pots with gamma isomer on gypsum at the rate of 200 lb. per acre, showing normal and abnormal growth.

Cytological effects.

Of the thirty normally developed roots studied, only one was completely unaffected by the insecticide while three had partially moribund meristems. A comparatively small number of abnormal cells was found in each root, the degree of effect being independent of the lengths of the roots and of the dose and method of application of the insecticide. The appearance of bridges in telophase and of pairs of resting cells joined by nuclear bridges was the main effect. The bridge may be a simple one involving only one chromosome, or a multiple one involving as many as

TABLE IV.

Frequencies of cells with fragment nuclei in roots grown in soil with varying doses of insecticides.

Treatment	Dose		Total No. of cells counted in six roots	Total No. of fragment nuclei	Range of No. of fragments per root
	gm./pot	lb./acre			
Flea beetle dust ; broadcast	0·15	200	15,756	101	8-41
Gamma isomer on gypsum ; broadcast ..	0·15	200	16,581	126	3-54
Flea beetle dust ; combine drilled ..	0·12	160	16,227	67	2-37
Flea beetle dust ; combine drilled ..	0·15	200	16,841	36	2-10
Gamma isomer on gypsum ; combine drilled	0·15	200	16,784	80	0-28

five chromosomes or occasionally the two daughter cells were almost completely fused together. In a total of 4,684 anaphases or telophases examined, 95 or approximately 2 per cent. were found to have bridges. A few late telophase figures had one or sometimes two nuclear fragments (Plate I, Fig. 4*g*) excluded after the cell wall had been laid down and fragment nuclei were found with resting nuclei. As shown in Table IV, the total number of nuclear fragments is small and about two is the greatest percentage of cells affected in one root. It is not sufficient to cause a serious loss, but the granular appearance of some daughter cells suggests that they do not survive. Occasional scattered metaphases and anaphases, multipolar telophases, and " sticky " contorted metaphases were found, but in all cases the numbers of such cells were so small that they cannot be given any more significance than that they indicate these doses in soil are not entirely without effects on roots which appear to be growing normally.

The three roots with partially moribund meristems had a quantity of faintly Feulgen-positive material in a state of disintegration, but many normal cells were in division. The meristems of the two abnormal roots illustrated in Fig. 5 and of one adventitious root were studied in detail. There was a quantity of faintly staining disintegrating tissue. The cell walls were unusually thick; in squashes the cells remained in compact masses, and there were well-developed xylem elements. The majority of the nuclei were small, deeply staining and moribund in appearance. A few cells were in division, they showed the same types of abnormalities as described for normally growing roots, and each root had a small area of polyploid cells. It is evident that the stunted growth was due to an independent toxic effect. This cannot definitely be attributed to the insecticide used, but since some of the viable cells showed abnormalities which have been proved to be due to the insecticide, it is clear that these roots had been in contact with a fairly high concentration, which was probably a local concentration due to uneven spreading. The deformation in growth compares very closely with that produced in wheat seedlings by Gavaudan and

Gavaudan (1940) with 1,3,5 trichlorobenzene and Hocking (1950) with the trichlorobenzenes and 2,4 dichlorophenol, both known to be breakdown products of hexachlorocyclohexane. The seedlings grown in Petri dishes with flea beetle dust showed no signs of independent toxic effects. If the insecticide breaks down in the soil a local concentration may be sufficient to produce this lethal effect, whilst the undecomposed insecticide will cause " stickiness " and polyploidy. The doses used in these experiments are the highest included in the effective dosage rates for the control of flea beetle. If they are evenly spread, it is clear that they can be used with little effect on the growth of the seedling, but with a slight cytological effect. In areas where concentrations occur, growth may be seriously affected or the healthy tissues may be polyploid or at least have a polyploid sector. Cytological effects, however slight, cannot be entirely ignored when crops are being grown for seed production, as they may lead to genetic alterations in the progeny. This aspect of the work is beyond the scope of this paper, but the results clearly draw attention to it.

EFFECT OF REMOVAL FROM THE INSECTICIDE.

The Petri dish experiments show that the lowest dose of the pure gamma isomer causes " stickiness " in telophase which may lead to the loss of nuclear fragments when the cell wall is laid down. In order to determine whether this " stickiness " is an important factor when the root is growing away from the insecticide and is in contact with a steadily decreasing dose, seeds were germinated as before and removed from the insecticide 24 hours after germination. The doses used are shown in Table V. On removal, the seedlings were washed for one hour in distilled water, put into a clean dish on clean filter paper and kept moist with distilled water. Root-tips were fixed at 24-hour intervals after removal.

TABLE V.

Mitotic index and frequencies of fragment nuclei in roots examined 24, 48, 72 and 96 hours after removal from the insecticide.

Time in hours between removal from insecticide and fixation	0·06 gm. gamma isomer on gypsum			0·03 gm. flea beetle dust		
	Total No. of cells counted	% dividing cells	No. of fragment nuclei	Total No. of cells counted	% dividing cells	No. of fragment nuclei
24	2,406	9·5	64	2,364	8·5	46
24	2,597	12·9	52	2,367	10·1	39
48	2,306	8·1	140	2,371	10·1	136
48	2,504	11·4	187	1,279	11·2	81
72	2,427	9·1	86	2,375	7·8	66
72	2,348	11·4	16	2,397	8·3	28
96	2,552	9·6	56	2,391	8·9	27
96	2,419	9·6	32	2,324	7·5	60

Two roots were counted in each group and the results are shown in Table V. It is assumed that the dividing cells would pass through one mitotic cycle whilst in contact with the insecticide, and would thereafter be affected by a steadily decreasing concentration or by the products of chemical reaction between the components of the cell and the insecticide. The mitotic index was appreciably lowered and had not returned to normal in the period of 96 hours under investigation, although a steady increase in the length of the root was maintained. The mitotic formula was only slightly irregular, which may be accounted for by the fact that these root-tips were partly diploid and partly tetraploid, with an occasional octoploid cell. At first many resting cells and many cells in late telophase were joined by nuclear bridges in pairs, or had protrusions and fragments from broken bridges, but later there were very few pairs. Some of the resting nuclei were large and irregular in shape and may be the consequence of multipolar spindle formation (Fig. 7*c* and *d*). The fragments usually occurred singly in the cell, less frequently in pairs, and in association with resting nuclei having one or more protrusions. They may arise in several different ways, but in all cases they appeared to be due to " stickiness " which delays the movement of one or more chromatids to the spindle pole, so that when the cell wall is laid down it cuts across the laggards (Fig. 7*a*). In some cells there was only one laggard which, when cut, produced one fragment and a protrusion. The appearance of two fragments in the same cell may be due to two laggards being cut or to the later divisions

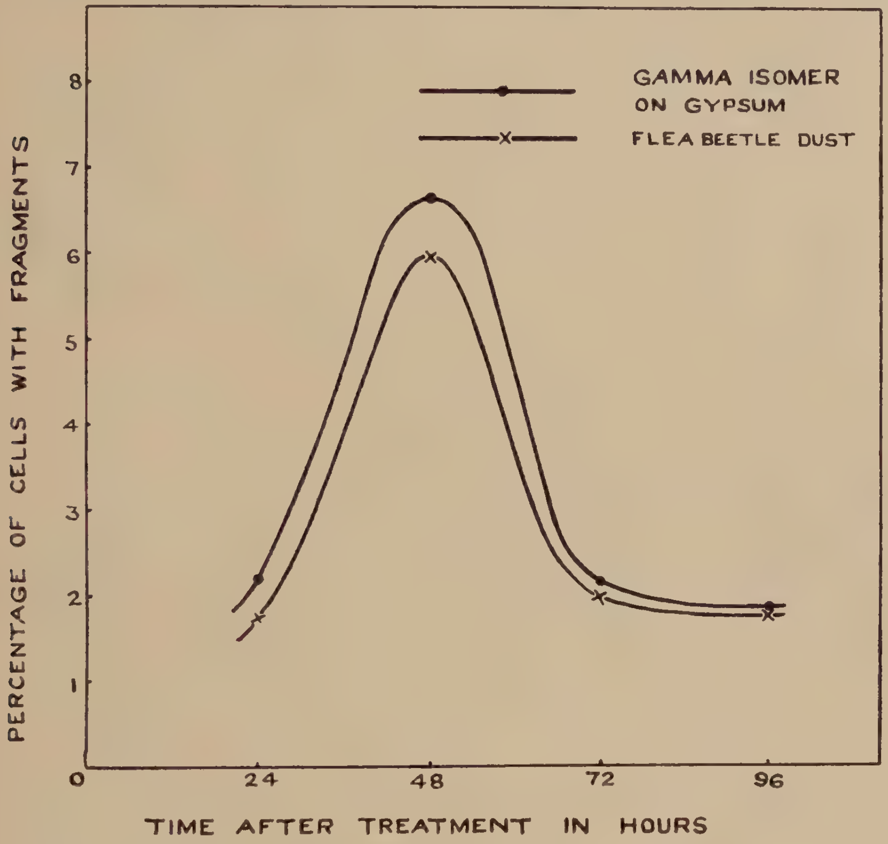


FIG. 6.

Graph showing the frequency of fragment nuclei at various intervals after removal from flea beetle dust and the gamma isomer of hexachlorocyclohexane.

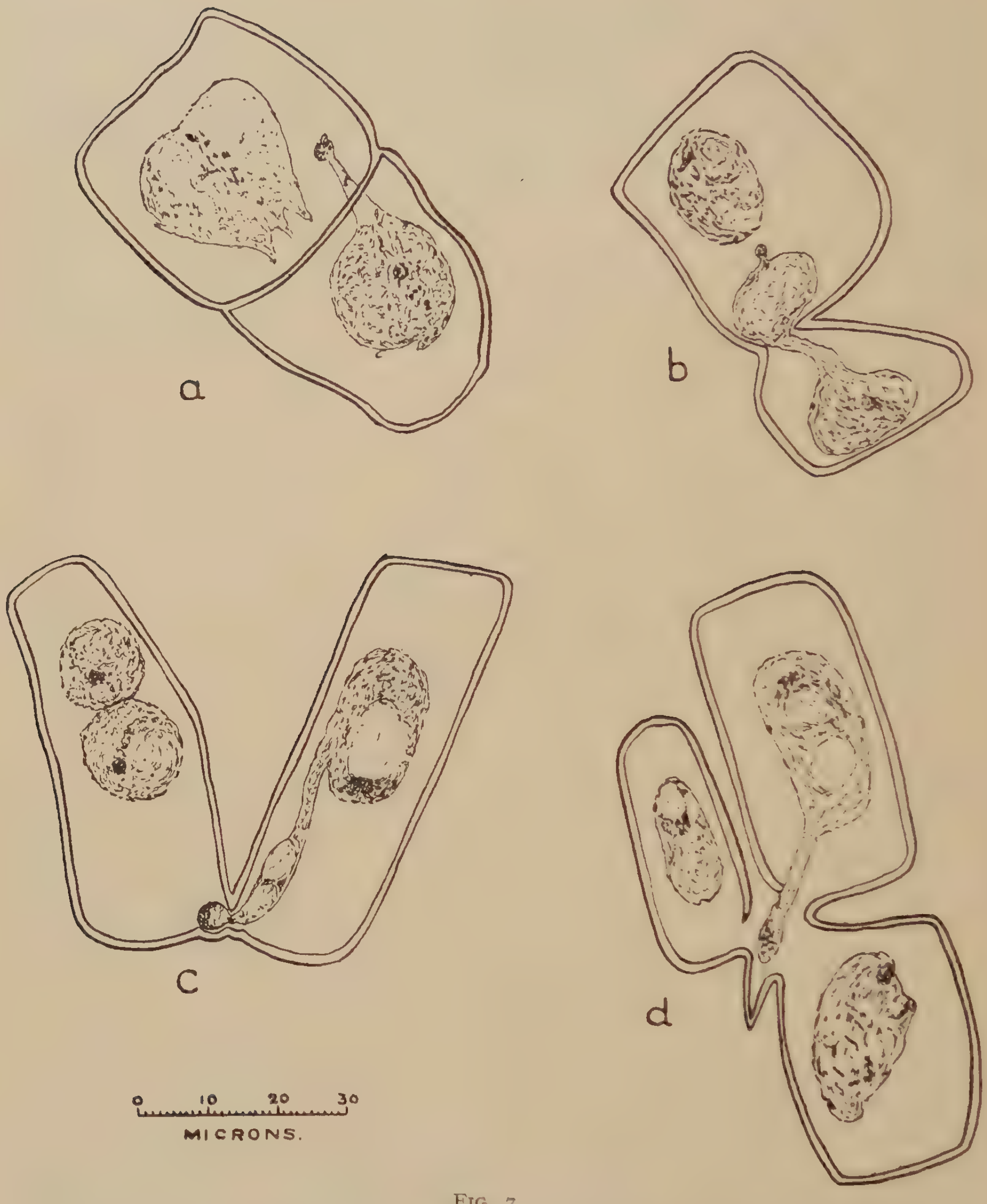


Fig. 7.

Abnormal cells illustrating results of "stickiness" and multipolar spindle formation. (*a* and *b*) 48 hours, (*c* and *d*) 72 hours after removal from 0·06 gm. gamma isomer on gypsum.
(*a*) Cell wall has cut across a laggard producing a fragment and protrusions.
(*b*) Bridge produced by numerous laggards impeding cell division.
(*c*) Bi-nucleate cell and protrusion impeding cell wall.
(*d*) Probably the result of multipolar spindle formation.

of a fragment produced at a previous cell division. In cells with several laggards a more complicated bridge was produced which is not cut by the cell plate, and either impedes cell division or produces a bi-nucleate cell (Fig. 7*b*). Where two daughter nuclei have a protrusion it may be due to one laggard forming a bridge between the two nuclei and the bridge being cut by the cell wall. At the next division one cell would have an acentric fragment, which is usually left out as a small fragment nucleus, and the other would have a true bridge chromosome which could be cut again. The fragments found at 72 and 96 hours, or even at 48 hours after treatment, may be of this secondary character.

In roots studied 24 hours after removal from the pure gamma isomer nearly all metaphase figures had the tetraploid number of chromosomes arranged on a spindle. In roots studied at longer intervals after treatment, metaphase figures had either the diploid or tetraploid number of chromosomes always arranged on a spindle, but there is often " stickiness " between the chromosomes, giving the figures an unusual, contorted appearance. In the case of the flea beetle dust, some metaphase chromosomes were arranged on a spindle after 48 hours, but it was not until 72 hours after removal that all metaphase chromosomes were to be seen arranged on a spindle. At 96 hours after treatment, when a new slender root-tip was maintaining a slow but steady growth rate, the proportion of tetraploid cells was small. Diploid cells definitely predominated and the new growth probably continued as diploid tissue, the root having suffered a severe check in growth.

Fig. 6 shows that the maximum effect of fragmentation of the nucleus occurs at 48 hours after treatment, which is probably during the second mitosis after removal from the insecticide. The percentage of cells involved, 6 to 7 per cent., is sufficient to account for the decreased growth rate, since it is probable that many of the deficient cells do not survive or at least have a reduced viability. The low solubility of the gamma isomer in water will accentuate this effect as the root grows away from the insecticide. It must be taken into account in using the gamma isomer for the production of polyploids and may in fact, preclude its use for such purpose. In addition to the loss of cells, some deficient cells may survive with an unbalanced genetic complement and some may be genetically altered.

THE ALPHA, BETA AND DELTA ISOMERS.

The doses of the alpha, beta and delta isomers separately mixed with gypsum, which were used in Petri dish experiments were those shown in Table I. The heaviest doses of the alpha and beta isomers had no effect on the growth rate and development of the seedlings, although they were not entirely without cytological effects. The delta isomer was comparable with the gamma isomer in causing polyploidy and seedlings grown with 0.06 gm. delta isomer on gypsum, and the heavier doses, had a decreased growth rate and the typical hypertrophy produced by spindle inhibitors.

The mitotic formula was determined for six roots in each group for those doses shown in Table VI. The effect of the delta isomer was comparable in every way with that of the gamma isomer (Figs. 2 and 3). It is clear that the production of polyploidy with a low dose of flea beetle dust is due to the combined effects of the gamma and delta isomers. Under the conditions of these experiments there was no evidence of dead cells, such as Carpentier and Fromageot (1950) presumably mean by their report of toxic effects in onion roots treated with the delta isomer, but it is impossible to compare the doses.

The highest dose of the alpha isomer was not strong enough to cause complete spindle inhibition, only about 5 per cent. of the metaphases having scattered chromosomes, and about 10 per cent. of the anaphases and telophases having simple or multiple nuclear bridges, but no metaphases were polyploid. Nybom and Knutsson (1947) found that the alpha isomer did not produce complete polyploidy in saturated solutions.

The beta isomer was almost entirely without cytological effects. There was no evidence of spindle inhibition and only about 2 per cent. of the anaphases and telophases had nuclear bridges.

TABLE VI.

Comparison of mitotic formulae for controls and roots grown in contact with the alpha, beta and delta isomers.

Treatment	Mean % prophases	Mean % metaphases	Mean % anaphases	Mean % telophases
Controls	41·5	11·9	4·4	42·2
Standard error of control mean ..	0·31	0·67	0·43	0·77
0·15 gm. α isomer on gypsum	40·5	15·8	4·7	38·6
0·15 gm. β isomer on gypsum	42·0	13·9	3·9	40·4
0·03 gm. δ isomer on gypsum	41·2	14·5	3·4	40·6
0·06 gm. δ isomer on gypsum	43·5	27·3	6·7	22·3
Sig. diff. ($P=0·05$) ..	3·24	2·59	1·97	7·0
Sig. diff. from controls ($P=0·05$)	2·38	2·34	1·66	5·18

EXPERIMENTS WITH *FRAGARIA VESCA*.

Insecticides containing crude hexachlorocyclohexane are frequently used on strawberry runner beds for protection against wireworm. The cytological effects of a proprietary wireworm dust, containing 0.45 per cent. of the gamma isomer, applied at the rate of 3 cwt. per acre, were investigated. This would distribute approximately 24 oz. of gamma isomer per acre. The parent plants were grown in a large pot and as they threw off runners, these were pegged down to root into smaller pots containing the insecticide, which was spread evenly on the surface of the soil and then " harrowed " in. Four days after rooting commenced, root-tips from these runners were fixed in acetic-alcohol ; aceto-carmine squashes were prepared and mitotic counts made of both control and experimental roots. The soil used was garden loam, partially sterilized by steaming at 180° F. and watered with rain water. The diploid *Fragaria vesca* ($2n=14$) was used to avoid the complication of working with material which was already polyploid and had a large number of very small chromosomes.

The mitotic formula for the control roots was determined from six roots taken from six different runners. To determine this formula 150-200 division figures, which is the greater part of the divisions in each meristem, were counted. The results are shown in the first line of Table VII. Twelve experimental roots were studied and these were taken from nine different runners. The lengths of the roots ranged from 0.8 to 3.5 cm. in both the control and the treated roots. It was not always possible to find 150 division figures in the experimental material, but the number of divisions counted is shown in Table VII.

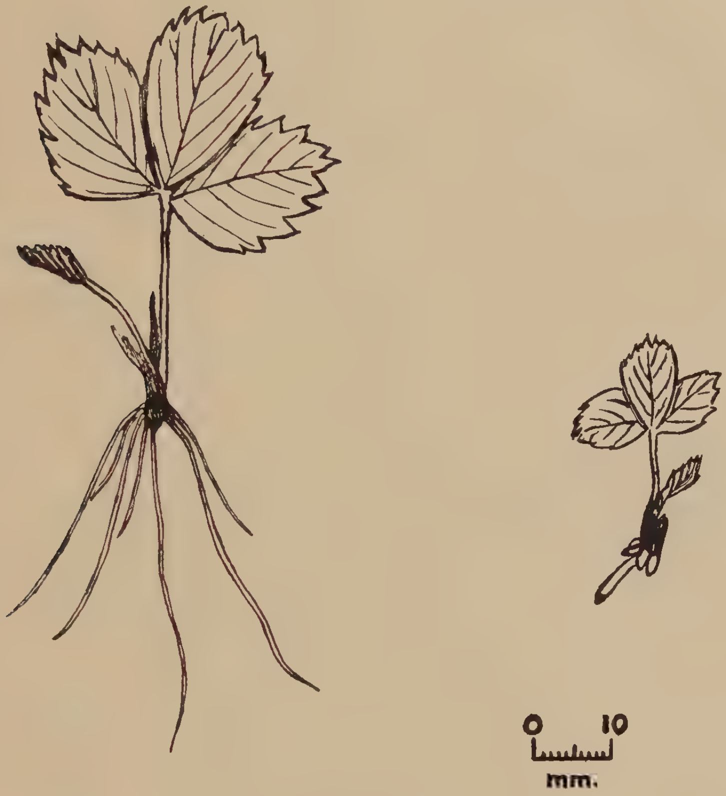


FIG. 8.

Strawberry runners four days after rooting in pots. Left—Control. Right—Runner grown with insecticide applied at the rate of 3 cwt. per acre.

Effects of the insecticide.

The experimental runners showed no difference from the controls in the number of roots put out but they often showed (Fig. 8) stunted growth and thickened roots. Only one root (No. 4) was found to be partially moribund. Seventy-five per cent. of the meristems studied showed some degree of polyploidy. The remainder were wholly diploid. The percentage of polyploid metaphases is given in Table VII.

TABLE VII.

Mitotic formula in roots of Fragaria vesca *and percentage polyploid metaphases in roots grown with a proprietary wireworm dust.*

Root No.	No. of dividing cells counted	% prophases	% metaphases	% anaphases	% telophases	% polyploid metaphases
Controls	150-200	12·9	31·5	2·8	53·6	
Standard error of Control Mean.		0·97	1·21	0·42	1·51	
1	160	13·1	79·0	2·5	5·6	86
2	109	14·6	61·3	2·8	21·2	58
3	163	11·0	36·0	3·0	50·0	46
4	45	8·9	51·0	6·7	33·5	39
5	169	14·2	38·0	3·6	44·5	20
6	147	6·1	38·8	2·1	53·0	7
7	144	11·0	40·5	5·5	43·0	3
8	157	7·6	37·0	3·8	51·5	3
9	107	7·5	25·3	4·7	60·0	3
10	176	10·8	40·5	2·9	46·0	0
11	168	8·9	35·0	3·0	53·0	0
12	178	9·5	34·5	3·9	52·5	0

Most of these cells had the tetraploid number of scattered chromosomes, a few were octo- or even higher polyploids, but the difficulty of counting large numbers of such small chromosomes in these cells makes it impossible to give definite figures. For the same reason it is impossible to state with certainty whether nuclear fragments were present or not. Although most of the polyploid metaphases were scattered, a small proportion had the tetraploid number of chromosomes arranged on a spindle. Normal diploid cells were found in all these roots, but many of the resting cells were giants, sometimes with one large nucleolus, but usually with several small nucleoli which had not fused together.

It is evident that the degree of polyploidy found in these roots is sufficient to be a significant factor in the commercial production of runners. It must, however, be remembered that pot-grown plants may absorb, on the average, more of the insecticide than would plants grown in the field, because of a more uniform supply of water. Partial polyploidy may cause distorted and slow growth in the affected runners, and any interference with the nucleus may lead to genetic alterations. A secondary runner which arises from the stock of an affected plant may be purely diploid or polyploid or a sectorial chimera. It would, therefore, appear to be inadvisable to apply these insecticides on runner beds used for maintaining " pure lines " or for stock production.

DISCUSSION.

The effect of the flea beetle dust on mitosis shows the hazards which may be involved in the widespread use of hexachlorocyclohexane as an insecticide. The gamma and delta isomers produce polyploidy, acting as spindle inhibitors, the alpha isomer has weak effects on the spindle while the beta isomer is without any such effect. This confirms the work of Nybom and Knutsson (1947) and Carpentier and Fromageot (1950). Whilst the immediate effect of autopolyploidy is to slow down development, other permanent effects such as changes from annual to perennial or sterile to fertile forms have been caused by doubling the chromosome number. Spindle inhibition is not, however, the only cytological effect and, from the agricultural point of view, may be the least important. The weaker effect, which resulted in " stickiness " and fragmentation of the nucleus, was caused by all the isomers separately, and was most pronounced with low doses of those inducing spindle inhibition. It was especially pronounced in roots examined at intervals after removal from the flea beetle dust and the gamma isomer, and these experiments probably compare more closely with the situation which is likely to arise in the field in roots growing away from a high local concentration. Although the " stickiness " is most apparent with the lower doses, it is sometimes evident as weak bridges between chromosomes in roots treated with higher doses (Plate I, Fig. 4*b*) and is probably only masked by the effects on the spindle. It is caused by other chemical agents which produce polyploidy, Östergren (1944), Levan and Steinegger (1947), Cornman (1947) and Levan and Tjio (1948). If the cell is regarded as re-acting as a whole to interference with any one constituent, the two effects may be the result of similar disturbances rather than separate effects and may throw some light on the causes of spindle inhibition. From the genetical point of view, " stickiness " and the consequent fragmentation would be as important as polyploidy. It might produce an enormous number of cytogenetic changes, and changes in characteristics which lead to species-formation are believed to originate as changes in the chromosomes. There is much experimental evidence to show that nearly all mutations induced by ionizing radiations are deleterious, so that it is reasonable to suggest that genetic changes induced by other treatments may often be of a deleterious nature.

The soil experiments with the onion introduce another factor, that of a lethal effect. The exact nature of this effect cannot be deduced from these experiments, but it would appear to be a result of contact with breakdown products of the insecticide. The cytological effects are small, but cannot be ignored. The strawberry experiments draw attention to the greater risk of polyploidy with a higher dose. High local concentrations of the insecticide are clearly dangerous. It is inevitable that they will occur in the field, but it is important that every effort should be made to minimize them. The most important point is that cytological effects occur in plants which appear to be unaffected and this must be borne in mind in growing crops for seed or, indeed, whenever the genetic constitution of the progeny should remain unaltered. The recent introduction of a fruit tree spray in the form of a dispersible powder containing the gamma isomer should be regarded with suspicion. In the commercial production of fruit it may be unimportant cytologically but, where young wood is used for scions in grafting, it introduces the factor of genetic changes. As it is recommended as a spring spray and would be applied at a time when meristematic cells are actively dividing, this factor should be taken into account in the nursery.

Of all the isomers present in crude hexachlorocyclohexane, it is firmly established that it is only the gamma form which is effective as an insecticide. As a result of the Petri dish experiments with the onion, the effects of the removal of the other isomers from the crude product may be summarized. The removal of the delta isomer would clearly approximately halve the possibility of causing polyploidy and reduce the risk of genetical effects from " stickiness " and fragmentation. The latter risk would also be reduced to some extent by the removal of the alpha and beta isomers. Slade (1945) stated that the beta isomer was the most stable, with a consistently low solubility and less reaction to dilute alkalies than the other isomers. Since its cytological effect in the Petri dish is so small, there would seem little to be gained by removing it. The removal of the alpha isomer would reduce cytological effects slightly more than would removal of the beta isomer but might have a greater effect in reducing the amount of the trichlorobenzenes produced ; this is the isomer which is present in the greatest quantity in the crude product. Hocking (1950) found that a mixture of trichlorobenzenes prepared by the breakdown of the alpha isomer caused plant deformation and ultimately inhibition of germination with relatively small doses. Its removal may, therefore, be important in reducing the risk of lethal effects.

If the gamma isomer alone is used, there still remains the risk of causing genetical changes and the risk of effects from breakdown products. Both risks are, however, considerably reduced by the removal of the other isomers. In considering the use of the gamma isomer for the production of polyploids, careful consideration must be given to the " stickiness " and fragmentation caused as the tissues recover from the treatment.

SUMMARY.

1. Onion seeds have been germinated in contact with a proprietary flea beetle dust containing crude hexachlorocyclohexane, and with mixtures of each of the isomers with gypsum at concentrations about equal to those in the flea beetle dust.

2. The doses used were equivalent to 40-200 lbs. per acre of flea beetle dust.

3. Doses without cytological effect had no effect on the development of seedlings, but doses inducing polyploidy reduced the growth rate and produced typical hypertrophy by 48 hours after germination.

4. The frequency of nuclear divisions was unaffected, but cells were delayed at metaphase, through spindle inhibition, by the gamma and delta isomers and by the dust, and partially by the alpha isomer.

5. Low doses caused only slight inhibition of spindle formation, but led to laggardliness in separation of some chromosomes and the appearance of " stickiness " at telophase leading to the exclusion of nuclear fragments. The latter effect was also caused by the beta isomer.

6. In pot experiments relatively high doses had little cytological effect. Affected roots showed some dead cells attributed to breakdown products of the insecticide. The risk of cytological effects with the doses investigated is small, but it cannot be ignored when crops are being grown for seed production.

7. The milder cytological effects were manifest for a period of at least 4 days after removal from the insecticide.

8. Strawberry (*Fragaria vesca*) runners rooted into soil treated with wireworm dust containing crude hexachlorocyclohexane, showed similar cytological derangements.

ACKNOWLEDGMENTS.

The task of counting resting cells was considerably lightened by the use of a foot-operated counting machine, designed and constructed by the author's husband. The author is grateful to Dr. R. E. Slade and all her friends for their helpful criticism and advice whilst carrying out this work. She is especially indebted to Miss Beakbane of East Malling Research Station, and to Dr. Catcheside and Dr. Riches of the Botany School, Cambridge, for constant help and for reading the manuscript. She also wishes to acknowledge the help of Dr. Pelc of Hammersmith Hospital in preparing the photographs, the help of Imperial Chemical Industries, Ltd., in supplying samples of the pure isomers used, and the generous support of the work by the Agricultural Research Council.

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REVIEWS

THE WEED PROBLEM: A NEW APPROACH. By F. C. King. (London: Faber and Faber. 1951. Pp. 164. Price 8s. 6d.)

In fruit orchards where the soil is cultivated, it has become the established practice to restrict cultivation to that part of the year when rainfall is less than evaporation and transpiration. Weeds are allowed to grow from August to March, as they can do no harm while the tree is not actively growing and are even beneficial by acting as a green manure crop. The attitude of the ordinary gardener, however, is to regard a weed as an enemy to be destroyed whenever and wherever it appears. In this book, Mr. King champions the weeds and advocates a system of no digging and less hoeing, believing that the weeds can be usefully employed as green manures and in compost-making. Under some conditions it may well be advantageous to allow a weed cover to remain, and this book will perform a useful function if it causes gardeners to pause and consider whether their present weed-destructive practices are always beneficial.

Unfortunately, this is not a scientific book. The author is a keen observer who interprets his observations on the basis of the tenets of the " humus school ", and there is a foreword by Lady Howard and an appendix by the late Sir Albert Howard on the Indore process of composting. Many of the arguments are based on false premises, and it is questionable how many of the claims would stand the test of scientific investigation. Particularly naïve is the dismissal of the " charge " that weeds compete with the crop for moisture and nutrients. The reader who is stimulated to try Mr. King's system will do well to note that his observations were made in a district where, as he admits, " the gardener has seldom to worry about a supply of water for his outdoor crops, for the rainfall is ample for all normal needs ".

Nevertheless, after allowing for the effect of local conditions on Mr. King's observations, and after discounting many of his arguments, there still remains an idea which deserves both serious consideration and scientific investigation.

D.W.P.G.

SCIENTIFIC HORTICULTURE.—VOLUME X. (H.E.A. Publications, c/o Gibbs & Sons, Orange Street, Canterbury. 1951. Pp. 240, illus. Price 10s. 6d.)

The work of the H.E.A. (Horticultural Education Association) is probably best known by its nine volumes of *Scientific Horticulture*. These were produced annually until the war, during which occasional papers appeared instead of the familiar volume. Publication was resumed in 1949 with Volume IX and the present volume covers the years 1950-1.

Twenty-three papers on various aspects of practical horticulture and the cognate sciences, together with a list of recent books, constitute the present volume.

The Director of the St. Ives Research Station gives an illustrated account of the twenty-one years' work on turf research carried out at that Station. Professor Wellensiek's University of London Lecture on Horticulture is reproduced with little amendment, while R. F. Martyr reviews the present system of horticultural education in the Netherlands.

Accounts of plant propagation in the various departments at the Royal Botanic

Gardens, Kew, and the Royal Horticultural Society's Garden, Wisley, make interesting reading and contain not a few promising lines for research. An introduction to the National Institute of Agricultural Engineering by E. R. Hoare is followed by an account of some of his department's work on protection from frost. The newly formed Agricultural Branch of the Meteorological Office is represented by L. P. Smith, whose account of Meteorology and Horticulture shows how the grower can benefit from increased co-operation with the meteorologist.

There are three papers on soils, by B. S. Furneaux on the soil as an environment, by D. A. Osmond on the present work of soil survey and classification in England, and by E. Crompton on the soils of North-West England.

Interesting papers on plant breeding in vegetable seed production by C. D. R. Dawson and on the work of the Mushroom Research Association by R. L. Edwards are followed by several papers dealing with commercial horticulture in different parts of the British Isles and one paper on horticulture in New Zealand. There is a table of contents. The illustrations consist of twenty plates and thirteen text figures.

This work of the H.E.A., in bringing together some of the recent advances and developments in horticulture in a readable form, will be appreciated by the teacher and advisory officer alike. A.P.P.

THE FRUIT YEAR BOOK, 1951-2. (Royal Horticultural Society, Vincent Square, London, S.W.1. 1951. Pp. 152, illus. Price 15s.)

This number goes from strength to strength, catering as it does for the commercial grower as well as for the amateur and consumer. Its dedication to Professor T. Wallace is a grateful recognition of his outstanding services to the industry, aptly, if very briefly, described by Mr. M. B. Crane in the introduction.

Articles by research workers in the United States and Canada on breeding fruits, and a most interesting discussion of the same subject by breeding experts in this country, show what is being done in this direction and the report of the Fruit Group brains trust covers many subjects.

The rootstock question in the U.S. differs radically from ours and Dr. Tukey does not suggest that most of the trees on seedling stocks are scion rooted, at any rate in the older orchards, therefore winter hardiness would presumably be a character of the variety rather than of the rootstock, owing to the practice there of root-grafting. The sulphur shortage is touched on by Mr. Marsh and Mr. Byrde, dealing with scab and brown rot and, unless more supplies become available, growers will be in considerable trouble. Dr. Massee deals with codling moth, a pest which is becoming more difficult to control. Some growers wonder whether a late-egg-laying race is not being developed. Very interesting and valuable notes are made by Mr. J. Rhodes and Messrs. Bracey on fruit-growing in the Northern counties and South Wales respectively, which will be of great value to both amateurs and growers in those areas. A useful account of walnut propagation in France is written by Miss Glenn. Amusing, instructive and valuable experiences of amateurs on heavy clay and chalk soils and how they dealt with their problems are given by Messrs. Crewdson and Saunders ; Mr. Hobbis describes a system of pruning cordons in gardens so as to obtain maximum results in the shortest time. Mr. Wilson deals also with troubles and faults of amateurs and the need for better pest control. The presence of other crops often prevents normal poisonous chemicals being used and probably frequent and copious dusting with derris and DDT powder is the safest means of dealing with many pests. Messrs. Abol Insecticide Company once marketed an ingenious little hand duster which could be used in the evenings by amateurs who, as Mr. Wilson points out, cannot always find the opportunity of spraying at the right time.

He also contributes a very interesting article on growing figs. In the eastern seaboard areas, it is common to find figs, many of which are old and fertile, grown as bushes with no training on walls. Medlars and gooseberries are dealt with. Mr. Spinks, by breeding for an increase in the vitamin content of blackcurrants, evidently studies the interests of the consumer.

Altogether this number is packed with most interesting and valuable information and is a credit to its Editor and Committee. W.P.S.

HEDGES, SHELTER BELTS AND SCREENS. By A. D. C. Le Sueur. (London: Country Life. 1951. Pp. 128, illus. Price 15s.)

This book is a most valuable contribution on a subject seldom tackled.

It contains a wealth of information which is well written in simple understandable language. Advice is given on the suitability of a range of shelter trees for various purposes, soils and positions, but a little more might have been said on providing temporary shelter for many of these subjects until established.

The chapters on hedging and the manual processes involved should prove invaluable to the farmer, and it is pleasing to note that the writer includes excellent costings on this subject. The author also relates his advice on shelter belts and hedges to the well-being of both crops and livestock on the farm and horticultural holding, and deals with their beneficial effects on the ever present problem of soil erosion.

The zones of protection provided by various heights and widths of shelter belts and hedges are fully discussed, with information on the degree of protection provided by a wide range of subjects.

Several references are made to the quick growing Monterey Cypress (*Cupressus macrocarpa*) but it should be pointed out that the new hybrid, *C. Leylandii* (*C. macrocarpa* × *C. nootkatensis*), is replacing this. In fairness to the author, however, he has pointed out the disadvantages of *C. macrocarpa*.

In the chapter on coast screens and shelter belts for mild areas a mention might have been made of subjects such as *Pittosporum crassifolium*, *Olearia Traversi* and *O. Forsteri*; even the common Elder and Escallonias are much used in coastal regions. Shelter belts and hedges of economic value that will bring in an income are sometimes planted by market gardeners. Hardy varieties of fruits and the foliage plants, e.g. *Pittosporum tenuifolium*, are also sometimes used in this way.

A most informative chapter is provided on hedges, trees and the law.

The book is splendidly illustrated and should find a place on the bookshelf of every agriculturist or horticulturist. H.W.A.

LUDDINGTON EXPERIMENTAL HORTICULTURE STATION. REPORT FOR 1950. Ministry of Agriculture and Fisheries. (H.M.S.O. 1951. Pp. 30, illus.)

The issue of this report—the first of any of the newly established Experimental Horticulture Stations—focuses attention on these new Stations and the type of studies to be undertaken. The first Horticultural Station to become established was at Luddington—a small hamlet almost in the centre of England—some two miles from Stratford-on-Avon and eight from Evesham.

Other Stations have been established in Yorkshire (with a daughter glasshouse Station in Lancashire) ; in Hampshire ; in West Cornwall (with a daughter Station in the Tamar Valley) and a remaining one is to be established in East Anglia, when a suitable site can be found. This chain of Stations it was expected would provide facilities for variety testing, field research, and experimental work in distant parts of England and under the varying climates enjoyed in these regions, thus making the results of much wider application than at present.

The report says the Luddington Station comprises 230 acres and has six distinct series of soils, some of which are suitable for the growing of fruit, vegetables and flowers and crops in frames. Of this area, 75 acres have been planted or reserved for fruit, 40 acres for vegetables and 12 acres for flowers.

In its first year (1950), the Station has carried out experiments in vegetables, salad crops and flowers of special interest to the market growers in the Midlands. Facilities have been provided for the National Institute of Agricultural Botany to conduct variety trials of Brassica crops, and for the Department of Agriculture, Oxford, to carry out experimental work on weed control in vegetable crops by selective herbicides. In future years no doubt the National Fruit and Vegetable Research Stations will use Luddington and the other Stations for extension field research work.

The Luddington Station is assisted by a Station Advisory Committee under the Chairmanship of Mr. A. G. Cutler—a prominent local grower. Other members are growers from the province, the Provincial Director, the Provincial Specialist Horticultural Officers, and the Directors of the Long Ashton Research Station, the East Malling Research Station and the National Vegetable Research Station.

This first report* is clearly and simply written. It gives a good account of the soil series of the farm, the proposed plan of cropping and a record of the experiments completed during 1950, as well as of those now in progress. Luddington has enjoyed a good start, excellent progress has been made and all horticultural growers will look forward to its continued success. H.V.T.

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* Obtainable on request from the Director, Luddington Experimental Horticultural Station, Stratford-on-Avon, Warwickshire.

STUDIES IN GROWTH AND DEVELOPMENT IN THE GENUS *FRAGARIA*

I. FACTORS AFFECTING THE RATE OF LEAF PRODUCTION IN ROYAL SOVEREIGN STRAWBERRY

By S. E. ARNEY
Monsanto Lecturer in Plant Physiology, University College, Cardiff

In order to survey the respiratory activity of strawberry leaves (Arney, 1947) records had to be kept of the time of emergence of many leaves produced during the 1939 and 1940 growing seasons. An analysis of these data indicated the desirability of continuing the observations over more growing seasons and suggested further experiments to test some of the provisional conclusions.

The surprising discovery that the plastochron interval of *Ipomoea* seedlings depends upon the date of sowing (Ashby and Wangerman, 1950) prompted an examination of the strawberry data to see whether this plant behaved similarly. Ashby uses the term "plastochron interval" for the interval in days between the times that successive leaves reach half their final areas. In the strawberry, which has a period of dormancy during the winter, it is preferable to use two criteria defined by the terms "interval between the times of emergence of successive leaves", and "interval between the times of initiation of successive primordia". The former is much more easily determined than Ashby's plastochron interval, but the interval between the times of initiation of successive primordia requires a knowledge of the number of primordia enclosed within the apex as well as the interval between the times of emergence of successive leaves, and is still being studied. The "rates of leaf production" now to be considered are based solely on the intervals between the times of emergence of successive leaves.

EXPERIMENTAL.

Material.

Royal Sovereign plants obtained from East Malling Research Station (M. 35 clone) were used for the 1939 and 1940 experiments. These plants were free from virus except for a mild form of crinkle. In subsequent work, in 1948 onwards, plants from the M. 40 clone were used. Some of these were propagated from plants originally obtained from East Malling and others were potted runners obtained from the Waterperry Horticultural School (stock certified by the Ministry of Agriculture and Fisheries). The 7-year-old plants used in 1948 were obtained from Mr. A. C. Painter of East Malling Research Station ; their age and their origin from the M. 40 clone is not in doubt. These plants were transplanted to Southampton in November, 1947, when they were already 6 years old.

All the results prior to 1949 refer to plants grown at Southampton but, in 1949 and the subsequent seasons, the plants were grown at Cardiff. Some runner plants and some 18-months-old plants were transplanted to Cardiff in February, 1949 and these supplied the data for the 1949 season. The 18-months-old plants were kept growing in pots at Southampton until they were bedded out at Cardiff.

Cultivation.

The plants used in 1939 and 1940 were all grown in 10 in. pots in good potting mould and were watered at frequent intervals with culture solution (James, 1936). Plants grown outside in 1940 were left in their pots which were placed in the ground with their brims level with the soil surface.

The 7-year-old plants were planted out without pots and were watered occasionally with 250 cc. of culture solution ; otherwise they received no watering except during one very dry spell in July, 1948. The soil at Southampton is a light gravelly loam with a very free drainage.

The plants at Cardiff were bedded out in a heavy clay loam which received an initial dressing of bone meal at 4 oz. to the square yard in 1949. At the end of 1950 this soil contained 300 p.p.m. of acetic acid-soluble P_2O_5 and 250 p.p.m. of exchangeable potash (K_2O) ; the pH at 6 in. was 7·5. In the spring of 1951 a dressing of 12 gm. sulphate of ammonia, 12 gm. potassium nitrate, 6 gm. of KH_2PO_4, and 6 gm. of K_2HPO_4 to the square yard was applied. The mixture of acid and basic phosphate was such as to give a buffering action at pH 7·0.

Records.

The day on which each leaf emerged from the shoot apex was decided by frequent examination of all plants. The criterion of emergence is necessarily arbitrary ; the leaf was assumed to have emerged when the light green of the young folded leaf blade first appeared, pushing up out of the enclosing sheath of the stipules of the next-oldest leaf. The period between the times of emergence of successive leaves is taken as a measure of the rate of leaf production.

TABLE I.

Seasonal change in leaf production rate of plants grown in a greenhouse.

	Mean interval* (in days) between times of emergence of successive leaves.								
	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.
A. ..	11·2 *1·5*	16·7 *1·6*	10·5 *0·5*	10·9 *0·5*	10·5 *0·5*	10·0 *0·4*	11·7 *0·4*	12·4 *0·4*	17·6 *1·3*
B. ..	7·5 *1·6*	19·2 *1·0*	11·7 *1·0*	12·0 *0·9*	9·9 *0·9*	11·2 *0·9*	12·1 *0·9*	10·5 *1·0*	17·5 *1·1*
C. ..	8·9 *1·3*	11·3 *0·6*	14·0 *1·1*	10·8 *0·6*	8·7 *0·6*	9·5 *0·3*	11·6 *0·5*	13·0 *0·5*	13·0 *0·6*
T. 1939..	—	—	—	—	—	73°	73°	67°	58°
1940..	54°	54°	65°	70°	75°	75°	72°	65°	60°
S. 1939..	3·4	3·2	6·3	7·0	7·5	5·0	6·5	6·3	3·3
1940..	1·0	4·4	4·4	8·2	9·6	6·7	7·7	6·4	3·6

* Standard errors of the means are given in italics under the corresponding mean.

A. 1939 season ; 1-year-old plants grown in pots. 14 crowns observed.
B. 1939 season ; 2-year-old plants grown in pots. 12 crowns observed.
C. 1940 season ; 1-year-old plants grown in pots. 14 crowns observed.
T = mean air temperature (°F.).
S = daily mean hours of bright sunshine.

THE SEASONAL CHANGE IN RATE OF LEAF PRODUCTION.

The mean rate of leaf production for each month of the growing season has been followed through several seasons, both for plants growing in pots in a greenhouse (Table I and Fig. 1), and in the open (Table II and Fig. 2). The monthly mean for each crown has been calculated, and the figures in the Tables and graphs are the means of all the monthly means for separate crowns, without any weighting for the number of intervals contributed by each crown.

The rate of leaf production varies greatly during the season, being much slower in spring and late autumn than in the summer. This trend is the same whether the plants are grown in the greenhouse or in the open but is more marked for the plants in the open. The young plants in the greenhouse in 1940 (Table I, C.) were derived from parents of different ages. A comparison of those runners derived from 1-year-old parents with those from 2-year-old parents showed no appreciable difference in the monthly rates of leaf formation, and no significant difference in the total number of leaves produced during the season.

It will be shown that leaf production rate is closely related to air temperature, and it seems likely that the seasonal change in leaf production rate can be attributed largely to the seasonal changes in air temperature. But a comparison of the results obtained in the greenhouse with those from outside shows that neither the onset nor the breaking of dormancy are completely determined by temperature. The emergence of leaves in the greenhouse commenced less than a fortnight earlier than

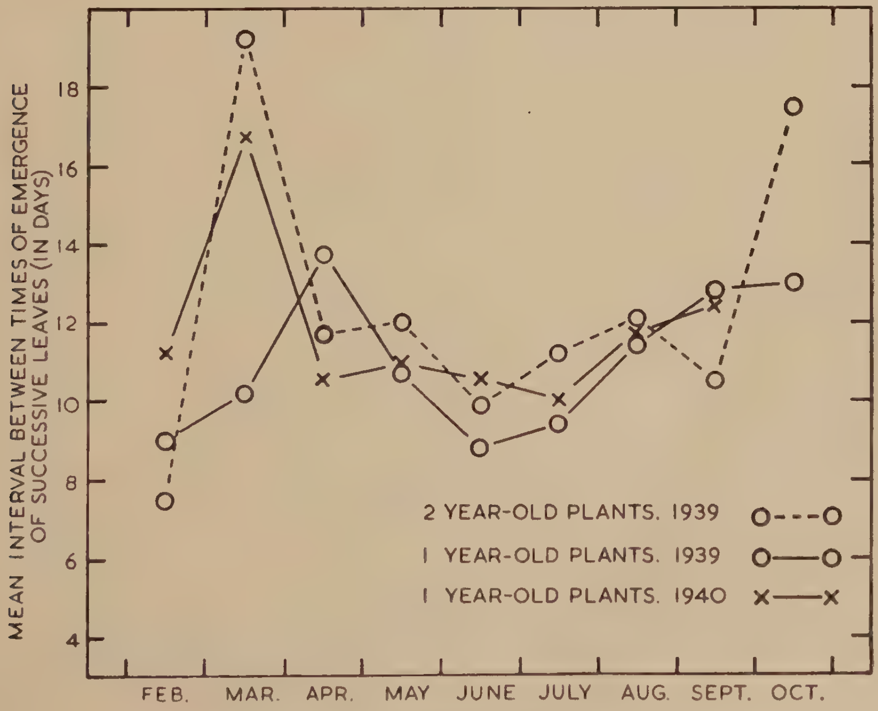

FIG. 1.

The rate of leaf production by strawberry plants in pots in a greenhouse.

outside, although the temperature in the greenhouse at the time was higher than the outside temperature for April; there was an appreciable decline in rate of leaf production in the greenhouse in the autumn, although the mean air temperature inside at that time was never lower than the outside temperature in June.

It seemed possible that the lowering of the rate of leaf production in the autumn might be the result of competition between the crowns of the parent plant and the young runner plants which are normally developing actively at this time. An attempt was made to test this with a few plants that were available in 1949, but no

TABLE II.

Seasonal change in leaf production rate of plants grown outside.

	Mean interval* (in days) between times of emergence of successive leaves								
	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.
A. ..	16·6	14·2	13·8	13·1	10·4	10·4	11·8	13·3	—
	1·0	*0·9*	*0·9*	*0·8*	*0·8*	*0·8*	*1·1*	*1·2*	—
B. ..	10·3	17·0	11·9	11·9	8·2	8·4	8·8	9·9	12·2
	1·0	*2·1*	*0·8*	*0·6*	*0·4*	*0·4*	*1·0*	*0·7*	*1·2*
C. ..	14·0	17·7	12·8	15·2	10·0	11·8	10·4	11·0	14·2
	0·1	*2·5*	*1·1*	*1·5*	*0·8*	*0·4*	*1·0*	*0·6*	*0·4*
D. ..	25·8	22·3	15·1	14·0	12·8	9·5	9·3	9·8	17·9
	1·6	*0·9*	*0·6*	*0·6*	*0·4*	*0·2*	*0·2*	*0·3*	*1·1*
E. ..	—	—	15·7	12·5	11·0	11·3	9·2	—	—
	—	—	*1·7*	*1·7*	*0·6*	*0·6*	*0·6*	—	—
T. 1940..	39·9°	44·7°	49·1°	55·5°	63·9°	60·7°	62·8°	57·8°	51·5°
1948..	—	—	50·5°	55·9°	58·9°	62·5°	60·8°	—	—
1949..	43·1°	43·4°	52·0°	53·0°	59·0°	56·2°	63·8°	62·3°	55·3°
1951..	40·5°	40·8°	45·9°	50·7°	58·2°	62·6°	59·7°	58·4°	50·6
R 1940..	2·9	3·2	1·2	0·3	0·2	3·9	0·0	1·6	4·5
1948..	—	—	1·8	3·8	2·3	0·8	3·6	—	—
1949..	2·4	1·9	3·0	3·7	0·6	1·3	2·3	3·6	8·7
1951..	4·4	4·1	3·5	2·5	0·7	1·0	4·6	5·4	1·9
S. 1940..	1·0	4·1	4·4	8·2	9·6	6·7	7·7	6·4	3·6
1948..	—	—	6·9	7·7	5·5	6·1	4·8	—	—
1949..	3·6	4·5	5·3	7·0	9·4	8·6	6·6	4·2	3·0
1951..	3·3	2·4	7·4	5·9	8·6	7·8	5·7	2·8	3·7

* Standard errors of the means are given in italics.

A. 1940 season; runners rooted in pots and plunged outside in October, 1939 and left in pots during 1940. 6 crowns observed.

B. 1949 season; runners rooted in the ground in 1948 and transplanted in February, 1949. 23 crowns observed.

C. 1949 season; 1947 runners grown in pots through 1948 and bedded out in February, 1949. 10 crowns observed.

D. 1951 season; 1950 runners bedded out in August and September, 1950. 30 crowns observed.

E. 1948 season; 7-year-old plants transplanted in November, 1947. 6 crowns observed.

T. = mean air temperature (°F.).

R. = total monthly rainfall, in inches.

S. = daily mean hours of bright sunshine.

difference connected with the removal or retention of runners was found. The possibility that factors of the environment other than temperature, such as photoperiods, may influence the rate of leaf production in the autumn is still under investigation.

The first leaves to emerge in early spring are often produced in rapid succession, so that the mean rate of leaf production for February may be much higher than that for March. This occurs in the greenhouse, as well as in the open, and the February rate for two of the sets of plants in the greenhouse (Table I, B. and C.) is as high as that recorded for any month in any season. It seems likely that there are at least two main factors interacting to produce this result.

Firstly, when the outside results are considered, the differences between the spring behaviour in the three seasons are seen to be related to temperature. In 1949 the latter half of February was warm and sunny but there was an exceptionally long cold spell in March. During the warm spell in February the first few leaves emerged, with only a very short interval between successive leaves, but the subsequent development of these leaves, and the emergence of the succeeding leaves was stopped by the cold frosty weather in March, so that, at the most, only one leaf emerged on each crown during the whole of March. In 1940, on the other hand,

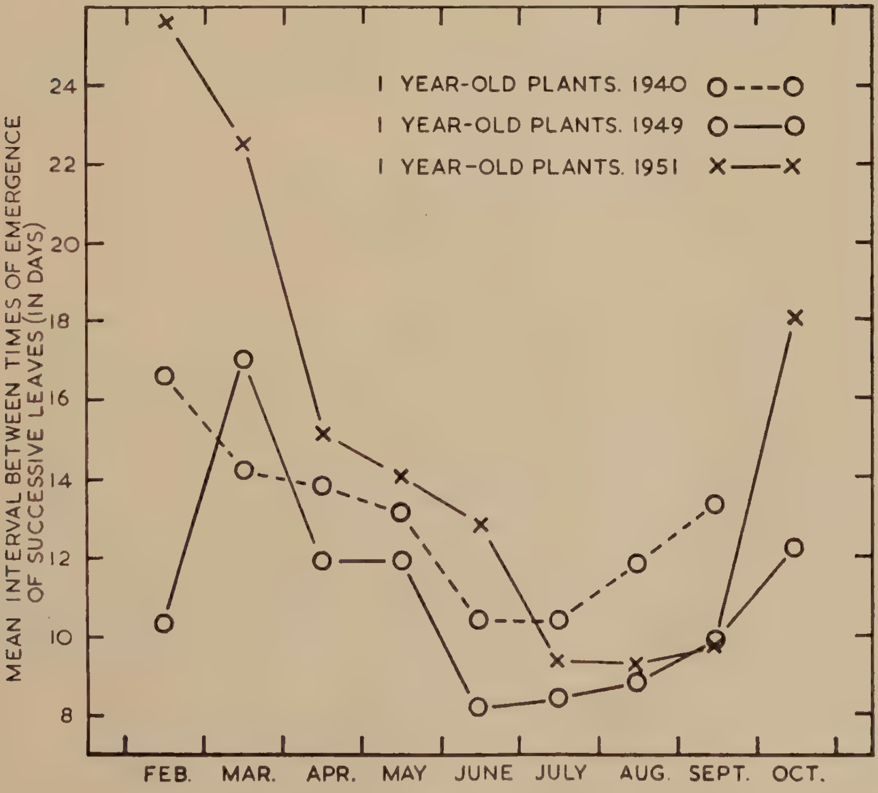

FIG. 2.

The rate of leaf production by strawberry plants grown in the open

February was very cold and March was comparatively warm ; few crowns produced even one leaf in February and most crowns produced at least two leaves in March, so that the March rate is higher than the February rate. In 1951, both February and March were as cold as February, 1940 and the rate of leaf production is very low in both months. These results show that mean air temperatures above 41°F. are necessary to enable leaf production to attain even a moderate rate.

Temperature, however, does not seem to be the only factor conditioning the rate of leaf production in February for, although the temperature in the greenhouse was 54°F. in both months, the March rate of leaf production is lower than the February rate in 1939 and again in 1940. There is a much greater drop in rate at the beginning of March, 1939 than in 1940; but results from 50 plants not included in Table I show that the difference in rates for February and March, 1940 is fully significant. It seems clear that a high initial rate is followed by a lower rate in March, both in the greenhouse and, in some seasons, in the open. Reference to Fig. 1 shows that the difference between the two months in 1940 is the result of a very high rate for February rather than a subnormal rate for March. In 1939 a subnormal rate for March is contrasted with a high rate for February. In the open the low temperature does not allow this very high rate to be developed in February. Unpublished results show that the successive primordia in the dormant apex at the beginning of February are more uniform in size than during the active growing season. Consequently successive leaves can develop to the stage of emergence in a comparatively short time when the temperature rises above 41°F. Thus, at least the first two leaves within the bud can emerge in quick succession during a warm spell or, in the greenhouse, in February.

ENVIRONMENTAL FACTORS AND LEAF PRODUCTION RATE.

Neither monthly rainfall nor mean daily hours of bright sunlight show significant correlation with leaf production rate.

Temperature.

The monthly mean air temperature and the monthly mean intervals between successive leaves outside in 1940, 1948, 1949 and 1951, taken together, show a fully significant negative correlation ($r = -0{\cdot}77$). Fig. 3 shows that the results obtained in the greenhouse do not fall on the same regression line as the outside results, and the indications are that a given temperature is associated with a leaf production rate which is lower in the greenhouse than outside.

The correlation between leaf production rate and air temperature might have no causal significance since the lower temperatures normally occur when the plants are either emerging from, or commencing, dormancy. The probability of a causal connection is enhanced by two instances in which temperature alone can be affecting leaf production rate. The rate of leaf production in the cold spring of 1951 is lower than in the warmer springs of 1940 and 1949. And the rate of leaf production in the greenhouse for the months February to May, is higher than outside. In both cases the differences are statistically significant.

Drought.

The monthly mean leaf production rates from June to September, 1940 were significantly ($P=0{\cdot}05$.) lower than the corresponding rates in 1949, and this suggested that the prolonged drought of 1940 might be responsible for this lower rate.

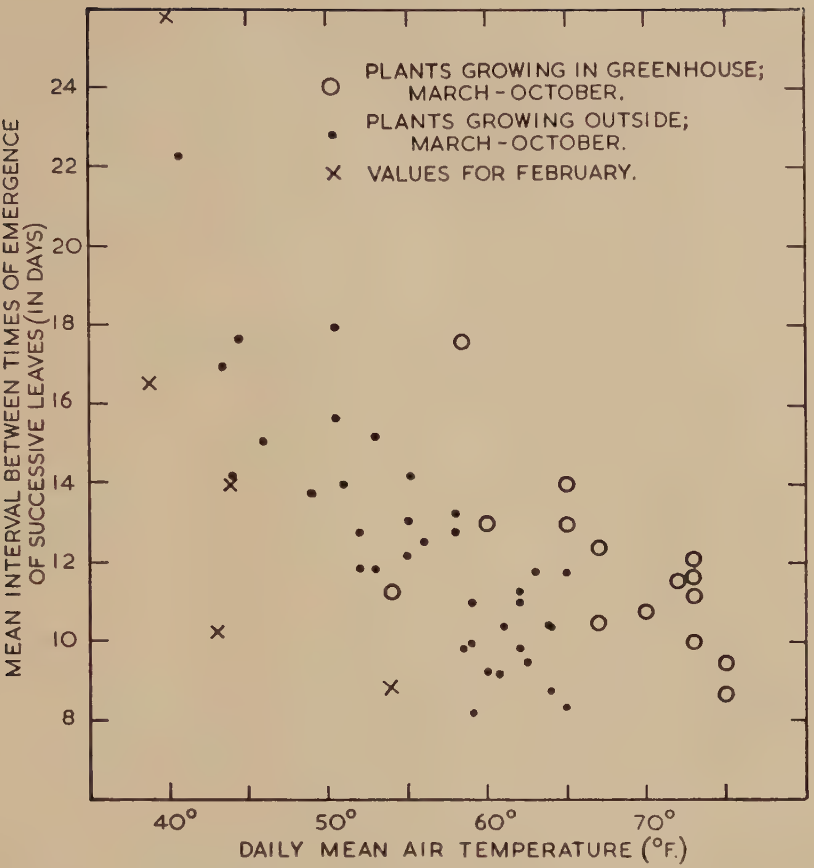

Fig. 3.

Leaf production rate and daily mean air temperature (°F.).

The 1951 results are intermediate in both rainfall and leaf production rate. The effect of water supply was further tested in 1949, when it became obvious that one row of strawberry plants was suffering from drought. This row was growing about two feet from the top edge of a bank occupied by *Solidago virgaurea*, a notoriously greedy plant and, farther back from the edge, at intervals of 2 ft. 6 in., were two other rows of strawberry plants. The three rows thus occupied positions with progressively drier soil conditions and the leaf production rates (Table III) show the expected relation to this change. The dry and medium rows both contained some two-year-old plants as well as one-year-old plants. From February to May there is no difference between the rates of leaf production of the dry and medium rows but, from June until August, the dry row shows a significantly ($P=0{\cdot}01$.) lower rate than the medium row for both the one-year-old and the two-year-old plants. On 6th September the dry row received a thorough watering with tap water (which contains practically no solutes in Cardiff), and the response of these plants was so immediate that the leaf production rate for the month was higher than for the medium and

TABLE III.

The effect of drought on the rate of leaf formation.

Age of plants	Water supply	Mean interval* (in days) between successive leaves				
		February-May	June-August		September	October
2 Years	Dry position.	14·3 *1·0*	15·4 *1·0*	Dry plants watered thoroughly	10·8 *0·9*	15·0 *0·9*
	Medium position.	14·8 *0·8*	10·7 *0·8*		11·0 *0·6*	14·2 *0·4*
1 Year	Dry position.	12·6 *0·9*	11·3 *0·9*		8·2 *0·5*	13·8 *0·5*
	Medium position.	12·5 *0·7*	8·4 *0·7*		10·2 *0·4*	15·1 *2·7*
	Normal position.	—	7·7 *0·3*		10·2 *0·4*	11·2 *0·8*
Average monthly rainfall		2·75	1·4		3·6	8·7

* Standard errors of the means are given in italics.

Plants grown in the open in 1949 ; June and July were extremely dry months. The plants growing in the dry position were watered thoroughly on 6th September ; other plants were not watered.

normal plants. This experiment shows that the rate of leaf emergence may be slowed down appreciably by abnormally dry conditions in the field and that the response to watering is very rapid. The assumption that the drought of 1940 was responsible for the lower rate of leaf formation in the summer of that year is supported by this result.

AGE AND LEAF PRODUCTION RATE.

Over the whole season of 1939 there was no significant difference between the average rates of leaf production of one- and two-year-old plants growing in the greenhouse. The rates of leaf production of older plants growing outside (Table II, C. and E.) are lower than for one-year-old plants, and the differences in average rates for the season are statistically significant. But it is not certain that these differences are related to age differences, as both sets of plants may have been suffering from recent transplanting. The 1949 two-year-olds had been transplanted in the February in which observations commenced, and the seven-year-olds had been transplanted in the November preceding observation. As strawberry plants are slow to recover from disturbance of their widespread root systems (Ball and Mann, 1926) it seems likely that both sets of plants suffered from inadequate water supply. There is thus little real evidence of any change in the rate of leaf production with increasing age of the plant, even after seven years' growth.

The interval between the times of emergence of the first few leaves of young runner plants is shown in Table IV. For the first two months, up to the time of severance, the runner has a somewhat longer interval than the parent plant, but the differences are only just significant and there is probably little divergence at all between the rates of leaf production of parent and runner. Severance from the parent, combined with transplanting, caused a marked reduction in rate of leaf production but recovery seems to be achieved within a month and the July-formed runners which were transplanted in September were producing leaves at least as fast as the parent plants in October. The runners formed in August were not transplanted until October and this was too late to enable them to return to a high rate of leaf production before the end of the season.

TABLE IV.

Initial leaf production of young runner plants (1949).

	Interval* (in days) between times of emergence of leaves				
	July	August	September	October	
Runners formed in July	11·0	10·7	15·0	10·6	
	0·5	*0·6*	*0·8*	*0·6*	
Runners formed in August	—	—	12·6	15·0	
	—	—	*0·6*	*1·2*	
Parent plants	8·4	8·8	9·9	12·2	
	0·4	*1·0*	*0·7*	*1·2*	
	Second interval	Third interval	Fourth interval	Fifth interval	Sixth interval
Runners formed in July	8·6	11·7	9·7	10·3	10·0
	0·5	*0·6*	*0·6*	*0·4*	*0·6*
Runners formed in August	9·3	13·8	12·0	12·1	—
	0·9	*0·7*	*0·6*	*1·0*	—

* Standard errors of the means are given in italics.

The second interval occurs between the second and third true foliage leaves of the runner. The two scale leaves, with vestigial laminae, are not counted.

When the intervals in the two sets of plants are compared on the basis of their serial order, there appears a characteristic irregularity in the rate of production of the first three or four leaves on the runner. It will be seen that the third interval is much longer than the second (the difference being significant at the 1 per cent. level) in both sets of runners. The fourth and fifth intervals are not as long as the third, but the difference is not statistically significant. It must be remembered that there is approximately six weeks difference in the time of initiation of the two sets of runners, so that the abnormally long third interval can hardly be associated with any climatic difference.

BRANCHING AND LEAF PRODUCTION RATE.

Most of the seasonal series have contained some plants with only a single crown, and the leaf production rate of these plants has been compared with the rate for plants with more than one crown (Table V.). The plants do not remain with only one crown throughout the whole of the first full growing season; most of the single crown plants produced a second crown before September, while most of the plants with several crowns (col. 3) had developed those crowns at the end of the previous season.

Only one season, 1949, showed a statistically significant difference between the two categories but the single crown plants have the higher figure in each comparison. Thus the formation of secondary crowns probably does slow down the rate of leaf formation slightly in the primary crown. Hence the effect of an increase in the number of crowns per plant is to increase the number of leaves formed *per plant* almost proportionately to the number of crowns formed. Each crown seems to behave as a separate unit and to obtain fairly adequate supplies for leaf formation, although the results do indicate slight competition between the primary and secondary crowns ; other observations show that the effect of competition may be much more marked in the case of leaf size.

TABLE V.

The effect of branching on the rate of leaf formation of the primary crown.

Experimental Series	Average interval between successive leaves for the whole season			
	Plants with one crown only		Plants with two or more crowns	
1939 ; 2 years-old ..	11·0	*1·2*	12·9	*0·3*
1939 ; 1 year-old ..	10·9	*1·3*	12·6	*0·3*
1940 ; 1 year-old ..	12·0	*0·6*	13·0	*0·35*
1948 ; 1 year-old ..	11·5	*0·7*	12·2	*0·7*
1949 ; 2 years-old "medium" ..	11·9	*0·5*	14·5	*0·5*
1949 ; 2 years-old "dry"	13·7	*2·1*	14·5	*1·5*

Standard errors of the means are given in italics.

Although there is some competition between crowns on the plant, there appears to be no competition between parent plant and runners (p. 76). Possibly this is because the runner plants develop their own root systems more rapidly and extensively and at a greater distance from the parent plant. Darrow (1930) found that there was an exponential increase in total leaf area throughout the growing season if the runners were included with the parent plant ; this would be expected in the absence of competition between parent and runners. Darrow showed that the total leaf area of his parent plants decreased during the production of runners. This need not be attributed to a slower rate of leaf formation ; it might be caused by the earlier death of mature leaves or by the reduction in size of the freshly formed leaves. Darrow obtained evidence of a reduction in leaf size of parent plants as a result of runner formation and it can be concluded that the competition between parent plant and runner affects leaf size but not the rate of leaf production.

DISCUSSION.

Ashby and Wangerman (1950) have shown that the plastochron interval of *Ipomoea* seedlings remains approximately constant for the first seven weeks of growth, at a value which is determined by the date of sowing. Strawberry plants cannot have a characteristic plastochron interval because this interval changes with season, but the behaviour of *Ipomoea* suggests that perhaps the *general level* of the leaf production rate might depend upon the date of initiation of the runners. Earlier-formed runners will produce larger plants with more crowns, and hence with more leaves, but it is the rate of leaf production *per crown* which should differ, to match the situation in *Ipomoea*. This only holds true for five out of the eight comparisons which have been possible, using runners produced from the same plant at different times during the season, and the strawberry plant therefore probably differs completely from *Ipomoea* in this respect. In any case it seems likely that the winter dormant period would obliterate any differences in leaf production rate that might be imposed by the date of initiation of the runners, just as it appears to obliterate the tendency to initiate flower primordia (Darrow and Waldo, 1934.)

It was suggested above (p. 76) that factors other than air temperature may be partly responsible for the low rate of leaf production at either end of the growing season. Ball and Mann (1926) emphasized the interlocking of the growth periods of the root and shoot of strawberry ; they found that active growth of roots occurs from August to December, and again in March and April. Floral primordia are initiated in August or early September (Unpublished work. See also Hill and Davis, 1929; Waldo, 1930 ; Roodenburg, 1939) and they develop rapidly during the autumn ; in March and April the runner primordia are developing and the inflorescences grow out and mature. Thus the two periods in which leaf production is slow, but not completely stopped, are the two periods during which the growth of other organs is most active ; possibly there is some connection between the two opposite growth trends.

On the whole, however, the rate of leaf production, which is markedly affected by temperature and to some extent also by the water balance, is not much affected by internal factors and by competition with other growth processes. Total leaf growth includes both leaf production rate and also leaf size and possibly it is the latter which is most affected by competition with other growth processes.

SUMMARY.

Records of the time of emergence of successive leaves on Royal Sovereign strawberry plants over a number of years show that the rate of leaf production is low in February, March and April, and in October and November, and reaches a maximum value of one leaf every 8 to 10 days during June, July and August.

The leaf production rate of plants grown in a heated greenhouse is significantly greater than the rate for outside plants, but only between February and May.

Leaf production rate is correlated with air temperature, but not with total monthly rainfall or mean daily hours of bright sunlight. Mean air temperatures below 41° F. stop the emergence of leaves almost completely.

Rainfall is only important after abnormally dry conditions which markedly reduce the rate of leaf formation. The dry summer of 1940 slowed the rate of leaf production appreciably. Watering after drought brings about recovery within a few days. Disturbance of the root systems by transplanting can also reduce the rate of leaf formation ; young runners recover within a month, but older plants may remain sensitive to dry conditions for a whole season afterwards.

For the first 7 years' growth no effect of age on rate of leaf production could be established.

The production of runners does not alter the rate of leaf formation of the parent plant, but the development of secondary crowns causes a small reduction in rate of leaf production *per crown*.

There appears to be a characteristic irregularity in the emergence of the first few leaves on the runner, with a long interval between the third and fourth leaves, but there is otherwise very little difference between the rate of leaf production of the parent and that of the runner during each month.

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BIOLOGY OF SOME PREDATORY INSECTS AND MITES ASSOCIATED WITH THE FRUIT TREE RED SPIDER MITE *(METATETRANYCHUS ULMI* (KOCH) *)* IN SOUTH-EASTERN ENGLAND*

II. SOME IMPORTANT PREDATORS OF THE MITE

By ELSIE COLLYER
East Malling Research Station, Kent

FORTY-FIVE species of insects and mites are predacious on the Fruit Tree Red Spider Mite in Essex orchards. A general account of this investigation and a detailed description of the most important predator in this country, the bug *Blepharidopterus angulatus* (Fall.), were given in Part I (Collyer, 1952). Of the remaining species, a few which occur abundantly in well-kept commercial orchards are described in this paper, and the other less abundant species will be described in Part III. The relative abundance of these species is very different in unsprayed orchards, and in a later paper the effect of the spraying programme on predators will be discussed. Of the extensive literature concerning the predators the most important references are included in this paper, but a more comprehensive list is given by Groves (1951).

The complete list of predacious species recognized up to the present time in Essex is as follows:

THYSANOPTERA	
Thripidae	*Thrips tabaci* Lind.
Aeolothripidae	*Aeolothrips melaleucus* Hal.
HEMIPTERA-HETEROPTERA	
Anthocoridae	*Anthocoris nemorum* (L.).
	Anthocoris nemoralis (F.).
	Anthocoris confusus Reut.
	Orius minutus (L.).
	Orius majusculus (Reut.).
Nabidae	*Himacerus apterus* (F.).
	Himacerus lativentris (Boh.).
Miridae	*Phytocoris tiliae* (F.).
	Phytocoris reuteri Saund.
	Phytocoris ulmi (L.).
	Camptobrochis lutescens (Schill.).
	Deraeocoris ruber (L.).
	Campyloneura virgula (H.-S.).
	Pilophorus perplexus D. and S.
	Blepharidopterus angulatus (Fall.).
	Orthotylus nassatus (F.).

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* Part of a thesis approved for the Degree of Doctor of Philosophy in the University of London.

Miridae	*Orthotylus marginalis* Reut.
	Capsus meriopterus (Scop.).
	Malacocoris chlorizans (Panz.).
	Psallus ambiguus (Fall.).
	Atractotomus mali (Mey.-D.).
	Plagiognathus arbustorum (F.).
	Campylomma verbasci (Mey.-D.).
NEUROPTERA	
Hemerobiidae	*Hemerobius humulinus* L.
	Hemerobius lutescens F.
Chrysopidae	*Chrysopa carnea* Steph.
Coniopterygidae	*Conwentzia psociformis* (Curt.).
	Conwentzia pineticola End.
	Coniopteryx tineiformis Curt.
	Semidalis aleyrodiformis (Steph.).
COLEOPTERA	
Staphylinidae	*Oligota flavicornis* Boisd.
Coccinellidae	*Adalia bipunctata* (L.).
	Coccinella septempunctata L.
	Stethorus punctillum (Wei.).
	Scymnus auritus Tb.
DIPTERA	
Cecidomyidae	Cecidomyid larva.
Syrphidae	Several species of Syrphid larva.
ACARINA	
Trombidiformes	*Anystis agilis* Bks.
	Cheyletus spp.
	Bdellid sp.
Parasitiformes	*Typhlodromus tiliae* Oudms.
	Typhlodromus finlandicus (Oudms.).
	Phytoseius spoofi (Oudms.).

(1) *Anthocoris nemorum* (L.).

(Hemiptera-Heteroptera, Fam. Anthocoridae).

According to Butler (1923) this species occurs all over Europe up to 70° N. latitude, and the whole of Siberia, Asia Minor and the Palaearctic regions of North Africa; it is common in Britain, and has been recorded in all but three of the English and five of the Welsh counties (Bedwell, 1945). It is a typically carnivorous insect and is found on a wide range of host plants, on trees, shrubs and many herbs. It occurs regularly and abundantly on fruit trees, both neglected and cultivated.

LIFE HISTORY.

A detailed account of this Hemipteron is given by Peska (1931). He describes the nymphal instars, and the life history in Poland which is very similar to that in England. There are two generations a year. In winter the imagines hibernate beneath the bark, among dead leaves, and in hedges and ditches. In March and

April they come out of hibernation and often congregate in large numbers on willow catkins. It was thought that only females of this species came out in the spring, and copulation therefore took place in the preceding autumn. This is probably the usual course of events and in 1947 and 1949 male *A. nemorum* were very scarce in the spring. In March, 1948, however, there were large numbers of both sexes present and many pairs were observed copulating. The females which come out from hibernation lay eggs from the end of March until June. The earliest laid eggs reach the imaginal stage in May, and therefore during May and June imagines of both generations can be present and, in June, eggs of two generations occur simultaneously. All stages are present throughout the summer from early April until September, with no clear differentiation between generations.

The female lays an average of two eggs a day, and may lay up to 200 eggs altogether. The egg is laid in the leaves of various plants, where it is inserted beneath the epidermis with the white, circular egg cap protruding (Fig. 1). Frequently the plant tissue surrounding the egg turns brown. Several days before it is due to hatch the egg changes from white to a deep reddish colour. The ventral side of the leaf is more often used for oviposition than the dorsal ; eggs are occasionally laid near the extreme margins of the leaves, especially under laboratory conditions ; they are also laid in the style and stamens of the flower, and in the opening buds. The time elapsing between oviposition and the final moult into the imago is from 30-35 days.

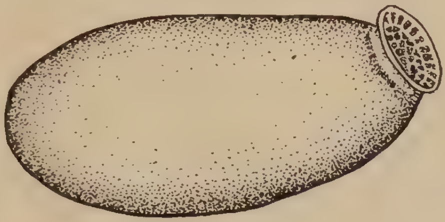

FIG. 1.
Egg of *Anthocoris nemorum* (L.), × 75.

FEEDING.

This bug has long been recognized as essentially carnivorous in habit. In the literature a wide range of prey is recorded, including apple suckers, aphids, cicadas, caterpillars, various gall midges, larvae and pupae of apple blossom weevil, and Mirid bugs. There are records of its feeding on the Fruit Tree Red Spider Mite in Norway (Schøyen, 1940), Finland (Listo, Listo and Kanervo, 1939), Russia (Vitzthum, 1943), Switzerland (Günthart, 1945), Germany (Andersen, 1947), and Holland (Geijskes, 1938 ; Kuenen, 1942). In England it was first recorded as a predator of the Fruit Tree Red Spider Mite by Massee and Steer (1929). *Anthocoris* species have been recorded in North America as predators of red spider mites (Garman and Townsend, 1938; Pickett *et al.* 1946).

Peska (1931) gives counts of aphids consumed by individual *A. nemorum*, and finds that on an average 500-600 aphids are sucked by each bug. In this investigation imagines have been found to suck as many as 45 adult red spider mites in an hour, but on an average their consumption per day is about 50 mites. The smaller nymphs consume about 20 mites per day, the older nymphs from 35-40. It is wholly carnivorous and feeds on a wide range of insects but, in cultivated orchards, mainly on red spider mites during the summer. Winter eggs of the mite are attacked in the autumn, in March and April before they hatch, and also when the overwintering imagines become active on warm days in the winter. In the summer the bug feeds to some extent on aphids and attacks other predacious species, particularly the inactive larvae of *Stethorus punctillum* (Wei.), *Oligota flavicornis* Boisd. and *Conwentzia pineticola* End., and is also cannibalistic. The bugs pierce the prey with their proboscis, insert the stylets, and suck them dry in a manner similar to that of *B. angulatus*. Whereas *B. angulatus* holds the proboscis vertically and attacks the prey from above, *Anthocoris* species pierce the victim from the side and hold the proboscis porrect. The proboscis of *A. nemorum* is short and stout, and during feeding is not bent when the stylets are inserted ; insertion must be due entirely to the action of the muscles attached to the bases of the stylets.

RELATED SPECIES.

Two species, *A. nemoralis* (F.) and *A. confusus* Reut. also occur occasionally in both cultivated and neglected orchards. They are similar in habits and life history to *A. nemorum* and both have a wide range of host plants. When they occur on apple they readily feed on all stages of the Fruit Tree Red Spider Mite ; they are entirely carnivorous, and feed on many other species of insects and mites.

(2) *Orius majusculus* (Reut.) (=*Triphleps majuscula* Reut.); *Orius minutus* (L.). (Hemiptera-Heteroptera, Fam. Anthocoridae).

These two species are very similar in appearance, and are found together in Essex orchards. Both occur throughout Europe and extend into Asia (Butler, 1923). They are widespread in England and Wales and have been recorded in 32 and 29 counties respectively (Bedwell, 1945). Both occur abundantly in orchards on cultivated and neglected trees, but *O. majusculus* is more plentiful than *O. minutus*.

LIFE HISTORY.

The life history and habits of the *Orius* species are very similar to those of *A. nemorum*. Again the majority of imagines which come out from hibernation in March and April are females, but males do occur and were numerous in 1948. There are two complete generations a year. The time from oviposition to the imago is from 24 to 30 days ; all stages are present simultaneously from April until August and there is no clear differentiation between the generations.

The eggs and nymphs of the two species of *Orius* are similar in appearance. The eggs are laid in the ventral side of the leaves of many host plants, always in the midrib, with the cap just projecting from the leaf surface. They are often laid in close batches of three or four, but each is laid in a separate cavity ; the surrounding plant tissue often becomes brown. The egg of *O. majusculus* is on an average 0·58 by 0·26 mm., and the egg cap is 0·12 mm. wide (Fig. 2), which is larger than that of *O. minutus*. Both are creamish white in colour. The nymphs of *O. majusculus* are larger than *O. minutus*. They are squat, with short legs and antennae, and are dull brown except in the first instar which is almost colourless. The imagines of the two species are distinct, *O. majusculus* being larger and relatively narrower than *O. minutus*; complete details of the differences between the two species are given by Butler (1923).

FEEDING.

O. minutus has been recorded as a predator of the Fruit Tree Red Spider Mite in Germany (Andersen, 1947; Zacher, 1922) and Switzerland (Günthart, 1945), but there is no account of *O. majusculus* feeding on red spider mites. In England they feed on many species of insects and mites, including other predacious forms and individuals of their own species. When red spider mites are abundant in orchards they form the staple diet, and all stages are attacked. In the autumn and spring, and occasionally during the winter, imagines suck mite winter eggs. Imagines can suck as many as 32 mites in an hour. On an average they consume 35 adult mites per day, the nymphs an average of 22 adult mites a day throughout the five instars.

RELATED SPECIES.

O. niger (Wolff) (=*Triphleps nigra* W.) is described by Bailov (1929) in Bulgaria as an important predator of thrips on tobacco; in addition he mentions that the species does occasionally feed on red spider mites. *O. niger* has been found on very rare occasions on apple trees in Essex. *O. insidiosus* Say is recorded in North America as a Fruit Tree Red Spider Mite predator (Garman, 1923; Lord, 1949; Newcomer and Yothers, 1929) and by many American authorities as a predator of related red spider mites on citrus and cotton.

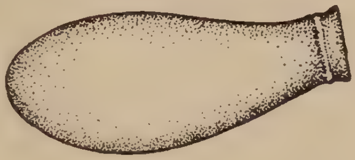

FIG. 2.
Egg of *Orius majusculus* (Reut.), × 75.

(3) *Campylomma verbasci* (Mey.-Dür).

(Hemiptera-Heteroptera, Fam. Miridae).

This species has only been recorded from Middlesex and Essex in Great Britain (Bedwell, 1945). In this investigation, however, it has been found abundantly in apple orchards of both Essex and Kent, and also in large numbers on oak. It is mentioned by North American workers as a predator of the Fruit Tree Red Spider Mite (Garman and Townsend, 1938; Gilliatt, 1935; Lord, 1949; Pickett, 1939), who find that it only occasionally appears in large numbers in apple orchards, where it may also sometimes cause considerable damage to the fruit. The only record of this insect in fruit orchards in Europe is that of Speyer (1933), who found two females on apple in the Lower Elbe but did not observe their feeding habits. In Essex it is prevalent in cultivated apple orchards, particularly in August and September when the second generation has developed, but it is rare in neglected ones. In orchards it feeds largely on the Fruit Tree Red Spider Mite, preferring the larger stages, and occasionally consumes aphids. It is partially phytophagous, but has not been found to cause damage in England. China (1932) describes the adult of this species.

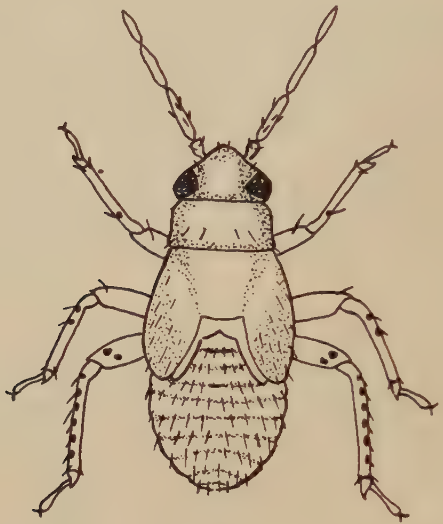

FIG. 3.
Nymph of *Campylomma verbasci* (Mey.-D.), instar V, × 20.

The nymph is smaller than any other Mirid species found on fruit trees. All instars are short and broad, with short legs and antennae (Fig. 3); they are a pale green-blue colour in all except the first instar which is more or less colourless. The abdominal gland is not visible, but the black lips of the pore are distinct between

TABLE I.

Campylomma verbasci (*Mey-D.*). *Average measurements in mm., of twelve individuals of each instar.*

Stage	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
Instar I	1·1	0·07	0·12	0·12	0·17	0·48
Instar II	1·4	0·10	0·17	0·15	0·19	0·61
Instar III	1·6	0·12	0·24	0·21	0·21	0·78
Instar IV	1·8	0·14	0·31	0·27	0·27	0·99
Instar V	2·3	0·17	0·35	0·30	0·28	1·10
Imago	3·4	0·17	0·60	0·44	0·28	1·49

the third and fourth abdominal segments. The body is covered with very short black and white hairs and, from the third instar onwards, there are black spines on the tibiae and femora. The antennae are very pale except for the basal joint, which has a somewhat darker apex in the fourth and fifth instars. The proportions of the antennal joints, which are a useful character for the identification of immature Mirids, can be seen in Table I.

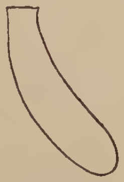

FIG. 4.
Egg of *Campylomma verbasci* (Mey.-D.), × 30.

LIFE HISTORY.

This species overwinters as an egg (Fig. 4) which averages 0·87 by 0·26 mm. and is embedded deeply in the young apple wood as in *B. angulatus*. Unlike the other predacious Mirids that occur on fruit trees, it has two generations a year. The overwintering eggs hatch during May; in 1948 nymphs were first seen on 9th May and in 1949 on 11th May. Development takes from three to four weeks, and first generation imagines are present from the beginning of June until August. Eggs are laid by these females in the young apple wood in a position similar to that of the overwintering eggs, although they are often incompletely embedded in the wood. These eggs hatch from the end of July until early September and the second generation of imagines appear from mid-August onwards and are found until late October.

(4) *Conwentzia pineticola* End.
(Neuroptera, Fam. Coniopterygidae).

An account of the larval characters of this species has been given elsewhere (Collyer, 1951), which proves it to be a distinct species and not merely a variety of *Conwentzia psociformis* (Curt.) as described by Killington (1936). The life history and feeding habits of both species are also described.

C. pineticola has two complete generations a year and often a third and, when this happens, a rapid increase in numbers occurs between July and September. The insect overwinters on the trunks of the trees as a cocoon within which it rests as a prepupa. Pupation occurs in March, and the first generation of imagines emerge in April. Eggs are laid on the leaves and branches (Fig. 6). In the autumn adults are active until November, and larvae until the end of December, both feeding solely on red spider mite winter eggs after the leaves have fallen. It is abundant on fruit trees in hot summers such as 1947 and 1949; its abundance is, however, spasmodic and in some years it is rare, as in 1948 and 1950. It seems to be associated solely with outbreaks of the Fruit Tree Red Spider Mite in commercial orchards, and has not been found on any other host plants or in neglected orchards.

C. pineticola is described by Listo, Listo and Kanervo (1939) as an important predator of the Fruit Tree Red Spider Mite in Finland, and larval Coniopterygids have been recorded as mite predators in Germany, Sweden and Denmark. *Conwentzia hageni* Bks. is a New World species which is predacious on various mites (Garman and Townsend, 1938).

RELATED SPECIES.

Three other Coniopterygid species occur in orchards in small numbers: *Conwentzia psociformis* (Curt.), *Coniopteryx tineiformis* Curt., and *Semidalis aleyrodiformis* (Steph.). They are all more frequent in commercial than in neglected orchards and are also found in association with various mites and aphids on other host plants, particularly hawthorn, sloe and oak.

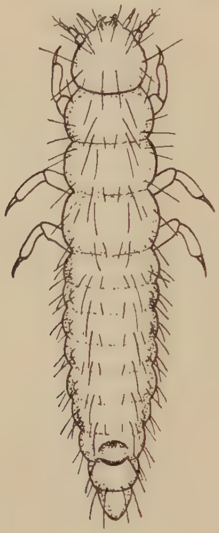

FIG. 5.
Larva of *Oligota flavicornis* Boisd., instar II, × 70.

(5) *Oligota flavicornis* Boisduval.
(Coleoptera, Fam. Staphylinidae).

O. flavicornis has been recorded as a predator of the Fruit Tree Red Spider Mite in Finland (Listo, *et al.* 1939); *O. pusillima* (Grav.) is of some importance in Switzerland (Günthart, 1945) and an *Oligota* species occurs occasionally as a predator on various red spider mites.

O. flavicornis is sometimes numerous in Essex commercial orchards, but its abundance varies from orchard to orchard, and from year to year. It only occurs in numbers when red spider mite infestations are severe, and is present infrequently on neglected trees. It is a small black shining beetle, about 1 mm. in length, with the abdomen tapering to a fine point ; when the insect is active it has the habit, characteristic of the Staphylinidae, of curling the distal portion of the abdomen up over the back. The larva is pale yellow and almost transparent, and bears a dorsal black hump on the seventh abdominal segment (Fig. 5). The eyes are small and red ; each segment bears a row of long white hairs. The legs are terminated by strong, curved claws. The larva is not very active, and is usually found crawling slowly over the ventral surface of the leaf. It passes through three larval instars and attains the length of about 2 mm., considerably longer than the adult beetle. The larval development takes from 8 to 15 days, then it drops from the tree to pupate just under the surface of the ground, where it remains from 10 to 15 days. The imagines live for many weeks, during which time the female lays from one to two eggs per day. In the laboratory, females have lived up to five weeks and laid from 40 to 50 eggs.

The egg is shining, with no superficial markings ; it is translucent and almost colourless when laid, and gradually darkens until it is dark orange just prior to hatching. Eggs vary in shape from ovoid to almost spherical, and often have portions of the surface flattened (Fig. 7). Measurements of twenty eggs give an average size of 0·32 by 0·28 mm. The eggs are laid on the ventral surface of the leaf and are covered, either partially or completely, with a pile of debris ; the female uses for this purpose cast, or sucked, skins of red spider mites, empty egg shells, leaf hairs, etc., and the egg is often obscured. The eggs hatch within 4 to 7 days, the life cycle of egg to adult occupying on an average 28 days.

LIFE HISTORY.

The imagines hibernate throughout the winter beneath the bark, or in vegetation beneath the trees, and these overwintering forms do not become active until May. They were first observed in Essex on 27th May in 1948, and 19th May in 1949. These imagines lay eggs through May and June, and a second generation develops, eggs and larvae becoming numerous again in August. This second generation is only a partial one, as the imagines, which mature late from the first generation eggs, may be found copulating but they do not oviposit before passing into hibernation. Larvae are rarely found in the orchard after the end of August, and the imagines all go into hibernation during September. The last dates that active *O. flavicornis* were noted in Essex were 21st September in 1948, and 19th September in 1949. Listo *et al.* (1939) record only a partial second generation in Finland.

FEEDING.

It is essentially a mite-eating species, and has not been observed feeding on other prey. All stages, even the smaller larvae, prefer active red spider mites to eggs but, if mites become scarce in September, winter eggs are readily sucked. The larva attacks its prey with the strong, curved mandibles and plunges them deep into the body. It remains perfectly still while sucking, and the red contents of the mite can be seen travelling down into the larval gut. Part of the gut contents are then regurgitated and forced back into the mite ; this usually takes place from five to seven times before the mite is completely sucked and the corpse rejected. The whole process takes from four to eight minutes, depending upon the size of both attacker and victim. The adult beetle chews the prey completely, leaving no remains.

(6) *Stethorus punctillum* (Weise) (=*Stethorus minimus* (Rossi)=*Scymnus punctillum* Wei.).

(Coleoptera, Fam. Coccinellidae).

Species of the genus *Stethorus* are of importance throughout the world where red spider mites occur. *S. punctillum* itself is recorded feeding on red spider mites in Germany (Andersen, 1947; Speyer, 1934; Zacher, 1922), Finland (Listo *et al.* 1939), Switzerland (Günthart, 1945), Holland (Geijskes, 1938) and Russia (Vitzthum, 1943). Kapur (1948) gives an account of the taxonomy and adult morphology of the European *Stethorus* species. To his list of references to the feeding of *Stethorus* species (including New World types) several may be added: *Scymnus minimus* Payk. on Fruit Tree Red Spider Mite in Holland (Kuenen, 1947); *Stethorus picipes* Casey on the same species in North America (Newcomer and Yothers, 1929); *Stethorus punctum* Lec. on the Fruit Tree Red Spider Mite and related mites by Garman and Townsend (1938) and many other authors in the United States of America. In most instances the beetles have been found feeding exclusively on mites and are regarded as one of the more important predators. In Essex *S. punctillum* is abundant in commercial fruit orchards but is rare in neglected ones; it occurs in hedgerows, usually in association with red spider mites.

The average size of the egg is 0·40 by 0·22 mm. It is cream in colour and oval in shape and the surface is pitted (Fig. 8). It is usually laid on the ventral surface of the leaves, occasionally on the twigs. The newly-emerged larva is dark brown in colour, with irregular black markings dorsally on each segment, and is covered with long hairs. The legs are relatively short and the larva is somewhat sluggish. It pupates on the leaves, generally on the ventral surface; the black pupa is attached by the anal end.

LIFE HISTORY.

These beetles hibernate as imagines, and emerge during May. There are two generations; the first eggs, laid in May and June, give rise to a generation in late June and July, which oviposit in July and August. As the adult beetles live from 6 to 8 weeks the generations are not distinct, and all stages are present from May to August inclusive. The incubation period of the egg is 5 to 8 days, of the larval stages 10 to 16 days, and of the pupa 5 to 7 days. On an average the development from egg to imago takes 24 days.

FEEDING.

In fruit orchards *S. punctillum* feeds entirely on mites, principally the Fruit Tree Red Spider Mite. All stages show a definite preference for the larger mite stages, but eggs are devoured especially by the larvae. In the autumn many mite winter eggs are eaten by this species. Where mite infestations are severe, and the winter eggs laid in a series of layers on sheets of webbing, larvae, pupae and imagines of the beetle have been found congregated in numbers in late September, entrapped beneath layers of webbing, where they feed solely on winter eggs. The latest date that larvae have been found still feeding in the field is 25th September. The imagines generally hibernate in early October, but are to be seen active and feeding much later than this on warm days. Likewise in the spring they are occasionally active long before their main period of activity.

The larval *S. punctillum* suck both eggs and active mites, leaving behind the empty egg shells and mite corpses; when feeding they perform a number of regurgitations before completely sucking their prey, like the larvae of *Oligota flavicornis* Boisd. The adult beetles consume the mites completely. Throughout the larval life an average of 24 mites a day are consumed; in the third instar the average is 31 mites a day. The imagines feed somewhat spasmodically, but the daily average is 20 mites. These counts were made when only adult female mites were provided as food for the beetles.

(7) ACARINA, Fam. Laelaptidae.

Of the predatory Acarina that occur on fruit trees the most important is a group of species belonging to the subfamily Phytoseiinae of the family Laelaptidae (Garman, 1948). The systematics of this group have only recently been worked out in detail. Of the species which occur in this part of England, three are important in fruit orchards; *Typhlodromus tiliae* Oudms., *Typhlodromus finlandicus* (Oudms.) and *Phytoseius spoofi* (Oudms.). These mites are very small and consequently not easy to find in the field, and are difficult to breed in the laboratory, so their study was postponed at the beginning of this investigation. Recently, however, it has become obvious that this group is probably potentially more important in red spider mite control than the larger insect predators, and a detailed study is being made of their biology. This work will be published elsewhere as soon as possible.

SUMMARY.

Forty-five species of insects and mites which feed on the Fruit Tree Red Spider Mite are listed. Details of the life history and habits of the species most abundant in commercial orchards are given in this paper, except *Blepharidopterus angulatus* (Fall.) which has already been dealt with fully in Part I.

The following species are described:

(1) Fam. Anthocoridae, of which *Anthocoris nemorum* (L.), *Orius majusculus* (Reut.) and *Orius minutus* (L.) are important.

(2) Fam. Miridae; *Campylomma verbasci* (Mey.-D.), a species which has two generations a year.

(3) Neuroptera, Fam. Coniopterygidae; *Conwentzia pineticola* End.

(4) Fam. Staphylinidae; *Oligota flavicornis* Boisd.

(5) Fam. Coccinellidae; *Stethorus punctillum* (Wei.).

(6) Acarina, Fam. Laelaptidae. *Typhlodromus tiliae* Oudms., *Typhlodromus finlandicus* (Oudms.) and *Phytoseius spoofi* (Oudms.) are abundant in this part of England.

ACKNOWLEDGMENTS.

The author thanks Dr. A. M. Massee for his help in this investigation, and Miss E. C. Thompson for the photomicrographs. Dr. H. H. S. Nesbitt of Canada very kindly identified the Laelaptid mites.

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PLATE I

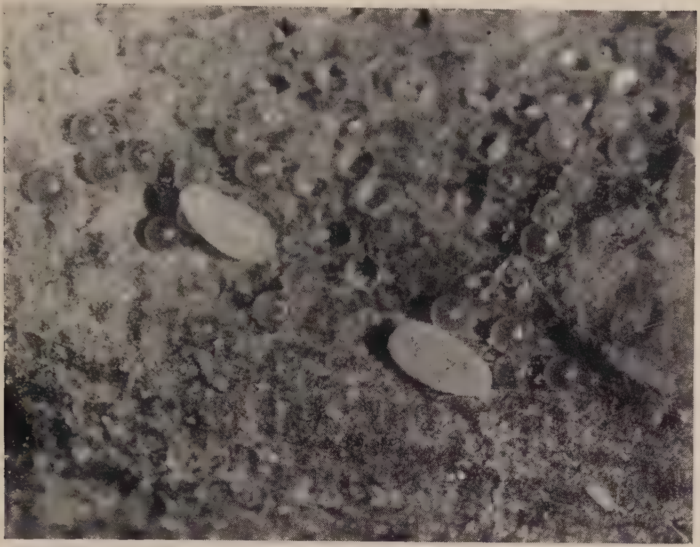

FIG. 6.

Conwentzia pineticola (End.)—eggs on apple twig.

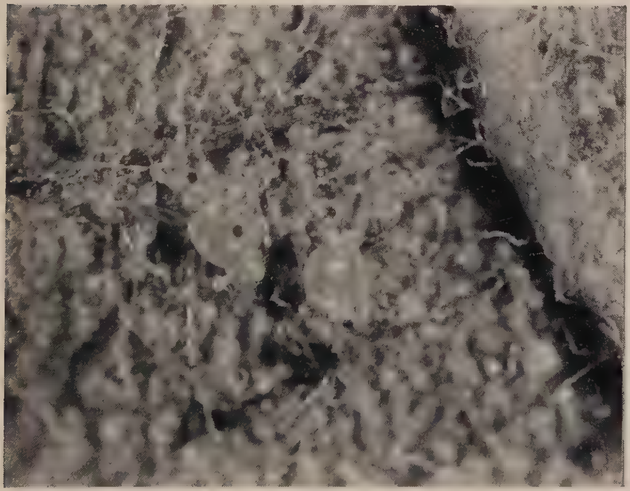

FIG. 7.

Oligota flavicornis Boisd.—eggs on ventral surface of apple leaf. × 32 approx.

PLATE II

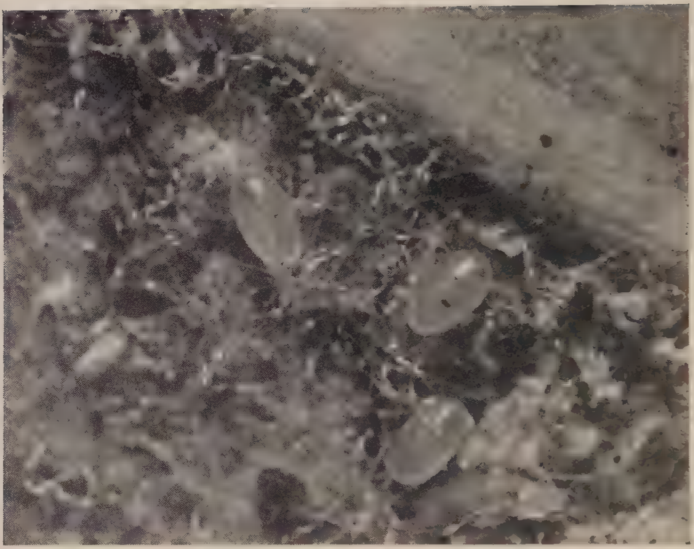

FIG. 8.

Stethorus punctillum (Wei.)—eggs on ventral surface of apple leaf. × 32 approx.

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BIOLOGY OF SOME PREDATORY INSECTS AND MITES ASSOCIATED WITH THE FRUIT TREE RED SPIDER MITE *(METATETRANYCHUS ULMI* (KOCH)*)* IN SOUTH-EASTERN ENGLAND*

III. FURTHER PREDATORS OF THE MITE

By **ELSIE COLLYER**
East Malling Research Station, Kent

A GENERAL account of this investigation and a description of the most important predator of the mite in orchards in this country, *Blepharidopterus angulatus* (Fall.), have been given in Part I of this series (Collyer, 1952). A list of the forty-five predators which have been identified was given in Part II (Collyer, 1953) with an account of a few species which are most common in well-kept commercial orchards. In this paper the remaining rarer species are described. The relative numbers of these species are different in commercial and neglected orchards, and the effects of the spraying programme on the occurrence of predators will be discussed in a further paper. A more comprehensive list of references to predators of the Fruit Tree Red Spider Mite and of other red spider mites is given by Groves (1951).

THYSANOPTERA.

In England the Thysanoptera are not important as predators but, elsewhere, various species of thrips are important natural enemies of mites. *Scolothrips sexmaculatus* Pergande is found in North America as a predator of the Fruit Tree Red Spider Mite (Garman, 1923; Garman, 1937; Garman and Townsend, 1938; Newcomer and Yothers, 1929), and in the United States as a predator on various mite species. Bailey (1939) gives an account of the biology of this species. Speyer (1938) attempted to import this thrips into England from California, on to carnations infested with red spider mites, but with little success. Various species of *Haplothrips* have been reported as predacious on the Fruit Tree Red Spider Mite in North America (Garman, 1923; Garman and Townsend, 1938; Lord, 1949; Pickett, Patterson, Stultz and Lord, 1946), and Finland (Listo, Listo and Kanervo, 1939).

In Essex *Thrips tabaci* Lind. and *Aeolothrips melaleucus* Hal. have occasionally been found attacking young stages of the mite. The former is generally regarded as phytophagous, and the latter has been recorded as an unimportant predator of the mite in Canada by Putman (1942).

HEMIPTERA-HETEROPTERA, Fam. NABIDAE.

Himacerus apterus (Fabricius) (=*Nabis apterus* (F.)).

This brown, agile and very predacious insect is found occasionally on fruit trees. It is more abundant in neglected than in commercial orchards, and occurs on many other host plants. It is probably wholly predacious in habit and feeds on many insects and mites. It occasionally feeds on red spider mites but prefers larger prey and often attacks Mirid bugs and members of its own species. *H. apterus* has not been recorded previously in fruit orchards. It passes the winter as an egg laid deep in the tissue of the young apple wood. The eggs hatch during May and June and the imagines are present from July until October.

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* Part of a thesis approved for the Degree of Doctor of Philosophy in the University of London.

The related species *Himacerus lativentris* (Boheman) occurs less frequently, and occasionally feeds on red spider mites. This species overwinters as an imago and lays its eggs early in the following summer.

HEMIPTERA-HETEROPTERA, Fam. MIRIDAE.

Many predacious Mirid bugs inhabit fruit orchards but none of them are as numerous as *B. angulatus* in the commercial orchards of South-eastern England. In neglected orchards, however, many of them are as abundant as *B. angulatus*, and some of them more so. The life history and immature stages of many of these species have previously been only incompletely described, although there are numerous records of the occurrence of imagines. The immature stages of several are difficult to distinguish from each other, especially the first instar nymphs. The length and proportions of the antennal joints form a reliable character, and tables of measurements are included for the species most easily confused. The nomenclature follows China (1943). For all species Oshanin (1909) gives details of the early literature, and for most of the species Butler (1923) gives the world distribution and Bedwell (1945) the distribution in the British Isles.

Phytocoris tiliae (F.).

Found on many trees, including lime (Reuter, 1883). Butler (1923) and Gulde (1921) recorded it on apple; the latter observed it predacious on caterpillars. In England it occurs in both commercial and neglected orchards, but is more abundant in the latter. It is mainly carnivorous and attacks many insect and mite species, including the red spider mite, and many predacious species.

Life history and notes on immature stages. The egg is, on an average, 1·28 by 0·37 mm. (Fig. 1) and is inserted in the young apple wood, where it remains throughout the winter. Eggs hatch from the beginning of June until early August. In 1948 nymphs were still present as late as 19th September. Imagines are found from July until October, and there is one generation a year. The fifth instar nymph is described by Butler (1923), and the characters he gives for this and other *Phytocoris* species apply also to the younger nymphal stages. A description of the imago is given by Douglas and Scott (1865).

Phytocoris ulmi (L.) and *Phytocoris reuteri* Saunders.

These are closely related species which occur in Essex in smaller numbers than *P. tiliae* on neglected trees but, with both species, apple is only an occasional host plant. The life histories of the three species are very similar. Douglas and Scott (1865) mention apple as a host plant of *P. reuteri*, but it has not previously been recorded as beneficial. The egg is 1·31 by 0·32 mm. (Fig. 1). *P. ulmi* is recorded on apple by Petherbridge and Husain (1918), and Butler (1923) deduces that it is probably carnivorous because it is found on such a wide variety of host plants.

Camptobrochis lutescens (Schilling).

Found on many trees and low-growing plants (Butler, 1923, Reuter, 1883) and was taken by Speyer (1933) in small numbers in orchards of Germany. Gulde

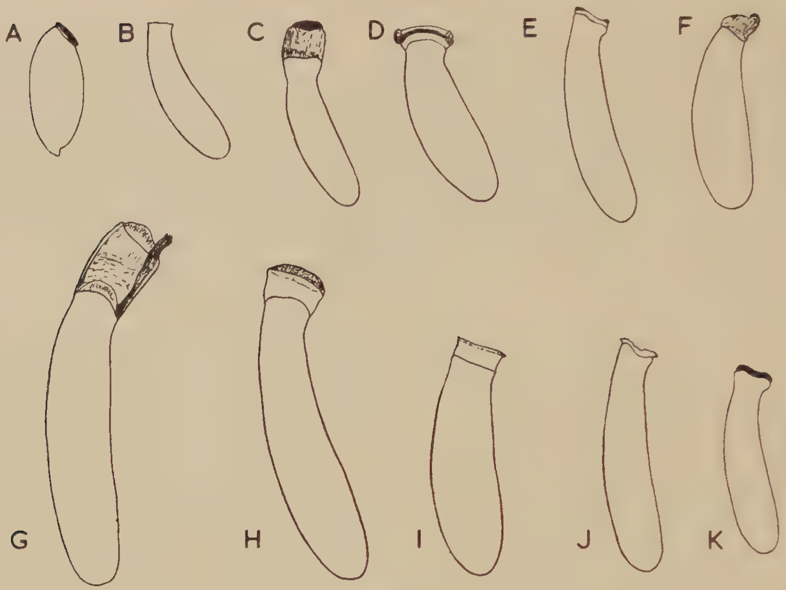

Fig. 1.

Eggs of some predacious Mirids. (× 25 approx.)

A. *Malacocoris chlorizans* (Panz.).
B. *Campylomma verbasci* (Mey.-D.)
C. *Capsus meriopterus* (Scop.).
D. *Orthotylus marginalis* Reut.
E. *Plagiognathus arbustorum* (F.).
F. *Camptobrochis lutescens* (Schill.).
G. *Deraeocoris ruber* (L.).
H. *Phytocoris reuteri* Saund.
I. *Phytocoris tiliae* (F.).
J. *Pilophorus perplexus* D. and S.
K. *Atractotomus mali* (Mey.-D.).

(1921) and Speyer (1933) both found it predacious, but not on red spider mites. In England it occurs regularly in both neglected and commercial orchards, but in small numbers. It is generally present on neighbouring trees and bushes of the hedgerow, where occasionally it is abundant, usually in association with an aphid infestation. It is a general predator, not very active, and prefers sedentary prey like red spider mites and aphids. It is partially phytophagous.

Life history and notes on immature stages. The imagines hibernate beneath the bark or among dead leaves under the trees. They become active in April and May, and oviposition continues over an extended period during the summer. Butler (1923) found that both sexes come out of hibernation and that impregnation took place in spring, but here only females have been found in the spring. The imago was described by Saunders (1892). Imagines are active from May to October, nymphs from early June until the end of August. The egg averages 1·05 by 0·24 mm. (Fig. 1) and is laid embedded in the young apple wood. The fifth instar nymph is described by Butler (1923). Nymphs of all instars are short and stout, with short legs and antennae ; they are white with reddish markings (Fig. 2).

Deraeocoris ruber (L.) (=*Capsus laniarius* Saund.=*Capsus ruber* L.).

Found on many trees, bushes and herbs (Butler, 1923) where it feeds on various insects and mites (Blatchley, 1926, Butler, 1923). In England a few occur in commercial orchards, but more in neglected ones where much time is spent in the undergrowth, particularly on nettles. It is entirely predacious, and prefers feeding on prey larger than red spider mites ; it is cannibalistic and attacks many other predacious species.

Life history and notes on the immature stages. The egg averages 2·02 by 0·34 mm. (Fig. 1), and is laid deep in the young apple wood where it remains throughout the winter. Nymphs begin to hatch in the middle of May and hatching continues for about six weeks. Imagines are present from early July until the end of August. Saunders (1892) describes the imagines and Butler (1923) four of the nymphal instars, all of which bear very large black setae.

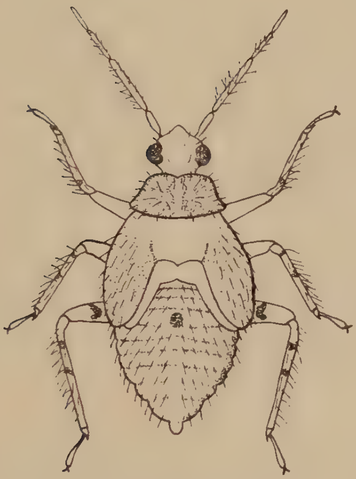

FIG. 2.
Camptobrochis lutescens (Schill.).
Instar V. × 10.

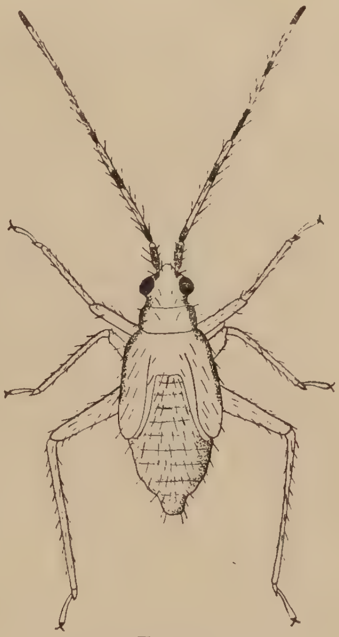

FIG. 3.
Campyloneura virgula (H.-S.).
Instar V. × 10.

Campyloneura virgula (Herrich-Schaeffer).

Found on many host plants (Butler, 1923; Reuter, 1883) and was recorded on fruit by Gulde (1921), who found it predacious on Woolly Aphid and caterpillars on apple trees. In Essex it occurs on apple and pear, particularly on the latter, and is more abundant on neglected trees than in commercial orchards. It has been observed feeding on various small insects and mites including the red spider mite. All instars are voracious, but adapt themselves to plant food when necessary.

Life history and notes on immature stages. Overwintering is in the egg stage and hatching continues from the first week of May until the end of August. The imagines are described by Douglas and Scott (1865) and the fifth instar nymph by Butler (1923). The nymphs are extremely delicate and slender, and are pale yellow with conspicuous red markings (Fig. 3). Compared with other Mirids, the antennae are relatively long (Table I).

TABLE I.

Campyloneura virgula (*H.-S.*). *Average measurements in mm. of 10 specimens of each instar.*

Instar	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
I ..	1·4	0·15	0·27	0·20	0·51	1·13
II ..	1·6	0·20	0·37	0·31	0·65	1·53
III ..	1·9	0·26	0·59	0·47	0·76	2·08
IV ..	2·3	0·34	0·94	0·64	0·88	2·80
V ..	2·7	0·43	1·36	0·85	1·02	3·66

Pilophorus perplexus D. and S.

Found on many host plants (Butler, 1923) including *Pyrus malus* (Gulde, 1921; Kullenberg, 1944) although it is never abundant on this plant. Petherbridge and Husain (1918) found it in apple orchards in the Cambridge neighbourhood, and considered it to be harmless. Lord (1949) records *P. perplexus* as a predator of the Fruit Tree Red Spider Mite in orchards of Nova Scotia. It is essentially carnivorous and has been observed feeding on aphids (Kullenberg, 1944; Leonard, 1928). In Essex a few only have been found in orchards, most frequently on neglected trees, where it is a general predator and feeds on a varied diet, including red spider mites and several species of aphids.

Life history and notes on immature stages. The egg is 1·29 by 0·29 mm. (Fig. 1). It is laid deeply embedded in the young wood of apple where it passes the winter. Nymphs hatch from the beginning of June for about three weeks, and imagines are active from early July until September. The nymphs and imagines are very ant-like in appearance ; the latter have been described by Saunders (1892).

Orthotylus marginalis Reuter.

Found on many host plants, in particular on species of *Salix* (Butler, 1923; Gulde, 1921; Kullenberg, 1944), and there are several records of its occurrence on apple and currant (Speyer, 1933; Wagner, 1937). According to Fryer (1916), it had then only recently changed its habits and appeared on the last host plants ; similar observations on this change in host plants were made by Speyer (1933). At one time *O. marginalis* was suspected of causing damage to apple foliage (Schøyen, 1914); Fryer and Petherbridge (1917) stated definitely that it caused no damage to apple, although it did live phytophagously on the leaves and fruit. This species is recognized as being at least partially carnivorous, and therefore beneficial, by Lehmann (1932), and Abraham (1936) gives an account of its feeding capacity on aphids ; Kullenberg (1944) regards it as both phytophagous and zoophagous, but from preference the latter. It has not previously been recorded feeding on the red spider mite. In Essex it occurs in small numbers in commercial orchards, and plentifully on neglected trees. In the latter environment the nymphs are generally on the fruit trees, but the imagines spend much of their time on the undergrowth. It also occurs on various other host plants, and is particularly numerous on *Salix*. It is predacious and feeds voraciously on red spider mites, aphids and other small prey ; it also exhibits cannibalism. In the absence of animal food, it feeds in a phytophagous manner on both the leaves and fruit of apple but causes no visible damage.

Life history and notes on immature stages. Abraham (1936) gives a biological account of this species. Of the Mirids that inhabit apple orchards it is the one which most closely resembles *B. angulatus*. The nymphs are yellowish in the first instar, in later instars green; a bluish tinge appears in the last two nymphal instars, which does not occur in *B. angulatus*. The orange abdominal gland is prominent dorsally, with a very indistinct opening between the third and fourth abdominal segments. The most conspicuous difference between the nymphs of *B. angulatus* and *O. marginalis* is the absence of the black " knees " in the latter species (Fig. 4). The antennae of *O. marginalis* are pale brown, all the joints much alike in colour and thickness. Throughout, they are shorter than in *B. angulatus* (Table II). In all instars the second joint is longer than the penultimate joint; in instars I and II the terminal joint is longest, in the remaining instars it is shorter than both the second and third joints.

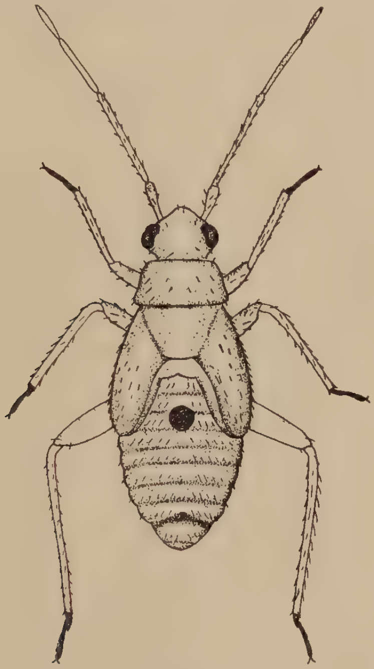

FIG. 4.
Orthotylus marginalis Reut. Instar V.
× 10.

The egg is on an average 1·07 by 0·32 mm. (Fig. 1), and is laid in the late summer in the young apple wood in a position similar to that of *B. angulatus*. Hatching of nymphs begins towards the end of April and occurs mainly in May. The last nymphs are still hatching at the end of May, when hatch of *B. angulatus* is just commencing, so that first instar nymphs of the two species occur simultaneously over a short period; the main hatch of *O. marginalis*, however, occurs a month

TABLE II.

Orthotylus marginalis *Reut. Average measurements in mm. of 12 specimens of each instar.*

Instar.	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
I ..	1·1	0·12	0·18	0·13	0·25	0·68
II ..	1·9	0·16	0·28	0·23	0·31	0·98
III ..	2·3	0·21	0·48	0·40	0·35	1·44
IV ..	3·6	0·33	0·77	0·57	0·48	2·15
V ..	4·2	0·46	1·30	0·85	0·59	3·20

earlier than that of *B. angulatus*. Imagines are present from early June until August. A description of the imago is given by Saunders (1892).

Related species. O. nassatus (F.) is larger and darker in colour than *O. marginalis* but their habits and life histories are very similar. It does not occur in commercial orchards but is plentiful on neglected trees and many other host plants, including *Salix*.

Capsus meriopterus (Scop.) (=*Heterotoma meriopterum* Scop.).

Found on many plants, from herbage to bushes and trees (Reuter, 1883). It has been recorded as predacious on caterpillars, aphids, etc. (Butler, 1923; Gulde, 1921; Kullenberg, 1944), but not on red spider mites. In South-eastern England it is less common in neglected than in commercial orchards, where it occurs in small numbers, and is often found beneath the trees on various weeds. It is mainly predacious, feeding on the Fruit Tree Red Spider Mite and less frequently on aphids; it sometimes feeds on the foliage and also pierces the fruit.

Life history and notes on immature stages. The life history is very like that of *B. angulatus*. The eggs are on an average 1·07 by 0·22 mm. and are laid in the young apple wood (Fig. 1). Nymphs hatch from the third week in May until September. The characteristic antennae distinguish it in all instars from other Mirid bugs (Fig. 5). The imago is described by Douglas and Scott (1865), and a brief account of the nymphs is given by Butler (1923).

Malacocoris chlorizans (Panzer).

Found on various plants (Reuter, 1883), and has been recorded in apple orchards by Massee and Steer (1929) in England, and Speyer (1933) in Germany. Massee and Steer record it as predacious on red spider mites but, referring to these observations, Speyer states that in the orchards of the Lower Elbe, red spider mites, aphids and small arthropods were extremely rare, and he considers the species to be wholly phytophagous under these conditions; he finds *M. chlorizans* the most numerous Mirid in these orchards. In South-eastern England it is present in small numbers in commercial orchards, and on derelict trees it is abundant. It occurs on other host plants, particularly *Salix* species. It is carnivorous in habit, and feeds mainly on all stages of red spider mites, but is partially phytophagous and can when necessary live entirely on plant material.

Life history and notes on immature stages. This species is somewhat exceptional among Miridae in that the egg is laid superficially and not inserted in the wood. It is either partially hidden beneath a bud or completely exposed on the surface of the wood, and is generally laid singly. The egg is yellowish, not shining, and somewhat flattened laterally ; it has a groove along the concave side (Fig. 1). It is 0·75 by 0·31 mm. The nymphs begin to hatch during June, and the earliest hatch observed in 1948 was 18th June and in 1949 was 25th June. Imagines are present from the second half of July until the end of September, in some years well into October. A brief description of the nymphs is given by Butler (1923). All the nymphal instars are extremely delicate, very pale green in colour, and with no markings ; they are slender, with long legs and antennae (Table III). The dorsal

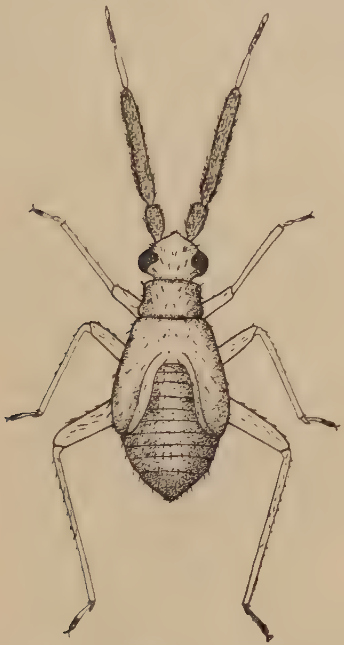

FIG. 5.
Capsus meriopterus (Scop.). Instar V.
× 10.

TABLE III.

Malacocoris chlorizans (*Panz.*). *Average measurements in mm. of 8 specimens of each instar.*

Instar	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
I ..	0·94	0·12	0·17	0·20	0·29	0·78
V ..	3·70	0·43	1·16	1·10	0·85	3·54

abdominal gland is not visible, but the pore can just be seen between the third and fourth abdominal segments. The imago is described by Douglas and Scott (1865).

Psallus ambiguus (Fallén).

Found on a number of host plants, most frequently on apple. In England it has been found in apple orchards (Butler, 1923; Fryer, 1916; Petherbridge and Husain, 1918; Saunders, 1892), and has also been found throughout the Continent. Although originally suspected of causing damage to apple foliage, Fryer and Petherbridge (1917) proved that this was not so. Most authors have recorded it as being at least partially carnivorous, and Petherbridge and Husain (1918) considered that it might be predacious on red spider mite eggs. In South-eastern England it occurs frequently on apple, more particularly in neglected orchards. It is predacious on all stages of the red spider mite, and also feeds on many other mites and small insects; it feeds on the plant tissue, but causes no visible damage and is unable to live on plant material alone.

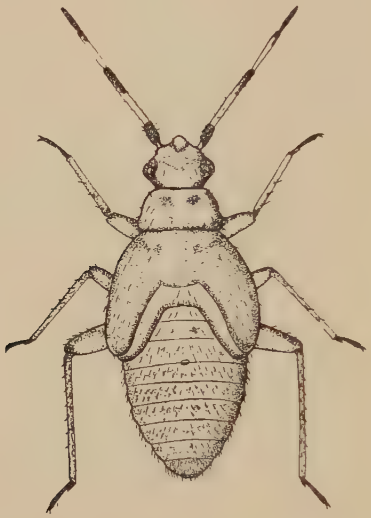

FIG. 6.
Psallus ambiguus (Fall.). Instar V.
× 10.

Life history and notes on immature stages. The eggs are laid, usually singly, in the young apple wood; Abraham (1937) has noted oviposition in young currant wood. Hatching takes place from the first week in April until the first week in May, and thus it appears earlier than any of the other Mirid predators. Imagines are present from mid-May until the end of June, by which time they have completed their oviposition. Butler (1923) gives a brief description of the fifth instar nymph. The nymphs are broad (Fig. 6), and the antennae and legs not very long (Table IV).

In the first instar, the first, second and fourth antennal joints are a pale orange colour, although this colour may not be very clear when they first hatch; in the second instar these regions become reddish-brown; in the fifth instar the basal

TABLE IV.

Psallus ambiguus (*Fall.*). *Average measurements in mm. of 12 specimens of each instar.*

Instar	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
I	1·2	0·07	0·15	0·13	0·22	0·57
II	1·7	0·12	0·24	0·20	0·26	0·82
III	2·3	0·19	0·34	0·25	0·29	1·07
IV	3·2	0·25	0·58	0·40	0·34	1·57
V	4·0	0·33	0·85	0·51	0·39	2·08

joint is dark drown or black, the second slightly less dark, the penultimate joint is pale with a black apex, and the terminal joint brown. The first instar nymphs are pale yellow when they emerge, and become gradually more orange ; the tip of the proboscis and the tarsi are black ; the abdominal gland is not visible, but in later instars the black lips of the opening become obvious between the third and fourth abdominal segments. From instar two the nymphs are mainly green ; they are more bluish-green than the nymphs of *O. marginalis* and *B. angulatus*, and much darker than *C. verbasci*. In all instars the body is clothed with short hairs, and the tibiae bear rows of black spines. The imago is described by Saunders (1892) ; there is a very wide colour variation, and the two sexes show differences in the antennae.

Atractotomus mali (Meyer-Dür).

This species is most frequently found on apple, also on *Prunus* and *Crataegus* (Butler, 1923 ; Gulde, 1921 ; Kullenberg, 1944 ; Reuter, 1883 ; Speyer, 1933) ; it occurs only occasionally on other host plants. Prohaska (1923) considered that it caused damage to apple similar to that by green apple aphid. Fryer (1916) in England recorded it as abundant in apple orchards where Capsid damage was severe, but later Fryer and Petherbridge (1917) confirmed that, although a phytophagous species, it caused no visible damage. There are several records indicating that *A. mali* is a predacious species ; Blatchley (1926) refers to it as feeding on aphids, and it has been noted feeding on caterpillars and various other insects (Butler, 1923 ; Kullenberg, 1944 ; Lehmann, 1932 ; Speyer, 1933). There is no previous record of its feeding on red spider mites. In South-eastern England, *A. mali* is abundant on neglected trees and occurs in small numbers in commercial orchards. Although all stages are readily predacious on small insects and mites, they are also partially phytophagous and can if necessary live in the absence of animal food. They are from preference mainly carnivorous and in commercial orchards feed largely on red spider mites, of which they attack all stages except the eggs. They are also cannibalistic.

Life history and notes on immature stages. The winter is passed as an egg, which is 1·02 by 0·24 mm. (Fig. 1) and is laid deep in the wood of the young apple shoots. The nymphs hatch from the beginning of May over a period of about four weeks, and were first observed in the field on 6th May, 1948, and 9th May, 1949. The imagines are present from the first week in June until the end of July. The nymph is briefly referred to by Butler (1923), and the species is easily recognized by its red colour and the nature of the antennae (Fig. 7). The first instar nymph, however, is very pale and does not develop the characteristic coloration of the antennae; although sometimes the second antennal joint is slightly red, this feature is not always developed. For measurements of the antennal joints, see Table V. In all nymphal instars the body is covered with fine white hairs except for the first two antennal joints which are covered with dense black hairs. The imagines are described by Saunders (1892). Immediately after the final moult they are dark red in colour like the nymphs, but as they mature they become very dark brown, sometimes almost black.

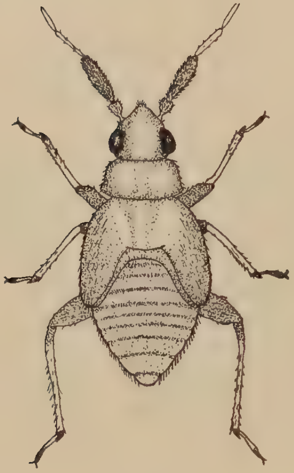

Fig. 7.
Atractotomus mali (Mey.-D.).
Instar V. × 10.

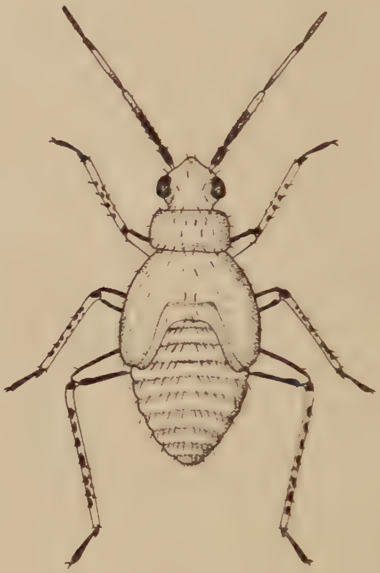

Fig. 8.
Plagiognathus arbustorum (F.).
Instar V. × 10.

Table V.

Atractotomus mali (*Mey.-D.*). *Average measurements in mm. of 12 specimens of each instar.*

Instar	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
I	1·4	0·12	0·20	0·17	0·24	0·73
II	1·9	0·14	0·28	0·23	0·26	0·91
III	2·4	0·17	0·39	0·31	0·29	1·16
IV	3·0	0·20	0·51	0·37	0·32	1·40
V	3·5	0·24	0·65	0·41	0·36	1·66

Plagiognathus arbustorum (Fabricius).

There is no previous record of this species occurring in fruit orchards. A great variety of host plants have been noted, nearly all of them low-growing herbs (Kullenberg, 1944; Reuter, 1883) and it has been found mainly on nettles. Kullenberg maintains that the species is wholly phytophagous in Sweden, despite reports by Butler (1923) and others that it is partially carnivorous. In South-eastern England this species is found in small numbers in both commercial and neglected orchards throughout the summer, and occasionally occurs in commercial orchards abundantly for a season. It is plentiful on other host plants in the neighbourhood, especially herbage. On apple it is essentially carnivorous and feeds mainly on red spider mites; it is also partially phytophagous but does not survive on plant material alone.

Life history and notes on immature stages. Abraham (1937) observed oviposition of this species on currant shoots in the laboratory, where he found that it laid eggs in batches in damaged regions of the shoot. In South-eastern England it readily oviposits in apple wood, but the eggs are usually laid singly or, more rarely, in pairs; the young shoots of apple are preferred and eggs are laid in a similar position to those of *B. angulatus*, but seldom in wounded tissues. The eggs are 1·19 by 0·29 mm. (Fig. 1). From the second instar onward this species is easily distinguished, but in the first instar it can easily be confused with *B. angulatus*. The first instar *P. arbustorum* is pale in colour, and the tarsi, tip of the proboscis and proximal end of the tibiae (the " knees ") are all black. The antennae are usually pale, occasionally the second joint is slightly darker. The chief distinguishing feature between the two species is that the abdominal gland and pore are not visible in *P. arbustorum*. The lengths of the antennae are different in the two species (Table VI).

TABLE VI.

Plagiognathus arbustorum (*F.*). *Average measurements in mm. of 12 specimens of each instar.*

Instar	Length of body	Length of antenna				
		Joint 1	Joint 2	Joint 3	Joint 4	Total
I ..	1·1	0·12	0·17	0·19	0·26	0·74
II ..	1·5	0·15	0·24	0·26	0·29	0·94
III ..	2·0	0·20	0·37	0·37	0·36	1·30
IV ..	2·6	0·27	0·73	0·66	0·45	2·11
V ..	3·7	0·34	0·81	0·71	0·46	2·32

The characteristic markings of *P. arbustorum* appear in the second instar. The basal joint of the antenna is black, with a light apex; the base and apex of the second joint are black, and the base of the third; the terminal joint is wholly dark. There are two black lines along the margins of the femora and, in addition to the black " knees ", the tibiae bear a row of dark spots and spines (Fig. 8). The nymphs are green, becoming a deep bluish-green in the later instars. The imago is described by Douglas and Scott (1865); it shows the same characteristic markings of the antennae and legs as the nymphs; in colour there is a variation from a very pale yellow to almost black. The nymphs begin to hatch in May, simultaneously with those of *B. angulatus*. Hatching continues throughout May and June, and imagines are active from late June until September.

NEUROPTERA. Fam. CHRYSOPIDAE.

Chrysopa carnea Stephens.

A detailed account of this species, including synonymy, distribution, description and life history, is given by Killington (1936). It is the only British Neuropteron known to hibernate as an imago. Associated with this habit is the striking colour change that some of the overwintering forms undergo; as the winter approaches they gradually change from bright green to a red or reddish-brown colour, while others remain green or only become slightly discoloured. During the winter they are sometimes active on warm days and in the spring the insects emerge and become green again.

The species occurs in varying numbers on fruit trees in Essex, most frequently in association with aphid colonies. The stalked eggs, laid singly in this species, are usually found on aphid-infested leaves. Both the adult and larval stages are carnivorous, and if the aphids become scarce they feed on red spider mites, especially if the infestation of mites is severe. Two generations a year occur. In the autumn, before they hibernate, the imagines often feed on the winter eggs of the mites.

This species has been recorded as a predator of the Fruit Tree Red Spider Mite in Finland by Listo *et al.* (1939). *Chrysopa* species have been recognized as predators of other red spider mites in Holland and widely in North America (Garman and Townsend, 1938; Kuenen, 1942). In Essex other species of *Chrysopa* are occasionally found on fruit trees, feeding on red spider mites and aphids, but are rare compared with *C. carnea*.

NEUROPTERA. Fam. HEMEROBIIDAE.

Various species of this family occur occasionally on fruit in Essex, but not in very large numbers. Of the imagines identified by F. J. Killington, the two most numerous species are *Hemerobius humulinus* L. and *Hemerobius lutescens* Fabricius. Both the imagines and larvae are predacious on the red spider mite in all its stages, and are to be found throughout the summer. Details of their biology are given by Killington (1936).

COLEOPTERA. Fam. COCCINELLIDAE.

Adalia bipunctata (L.).

This species has been recorded as a predator of the Fruit Tree Red Spider Mite in England (Massee and Steer, 1929), Canada (Ross and Robinson, 1922) and Finland (Listo *et al.*, 1939). In Essex it occurs spasmodically in both neglected and commercial orchards, and it is occasionally abundant in the latter, particularly when there is an attack of aphids. Both imagines and larvae are wholly predacious; they prefer aphids, but also attack all stages of the Fruit Tree Red Spider Mite when the infestation of mites is heavy.

Coccinella septempunctata L.

This species, like the preceding one, is essentially aphidivorous and is attracted into commercial fruit plantations by aphid infestations. The larvae, however, feed on all stages of the red spider mite if no aphids are available. Both species overwinter as imagines and although they are frequently active in late autumn, early spring and on warm days throughout the winter, they very rarely feed on red spider mite winter eggs.

Scymnus auritus Tb.

This species normally inhabits oak, but occasionally occurs on fruit trees where it is predacious on red spider mites.

DIPTERA. Fam. SYRPHIDAE.

Larvae of several Syrphid species have been observed feeding on all stages of red spider mite in Essex. The Syrphid eggs are frequently laid near aphid colonies, and the predacious larvae feed mainly on aphids; in the absence of aphids they consume many mites.

ACARINA. TROMBIDIFORMES. Fam. ANYSTIDAE.

Anystis agilis Banks.

This species has been recorded as a predator of the red spider mite in Holland (Geijskes, 1938), and North America (Garman and Townsend, 1938; Gilliatt, 1935; Lord, 1949). It is a large red mite which occurs occasionally on cultivated fruit trees in Essex and more commonly on derelict trees; it frequents many other bushes and trees. It is wholly predacious and feeds on various mite and insect species; when feeding on the red spider mite it prefers the larger and active stages. It moves rapidly over the leaves in a curious circular motion, and if it chances upon suitable prey this is grasped by the mouthparts and sucked dry, while the mite continues moving erratically over the leaf.

Several other mite species of the families Bdellidae and Cheyletidae have been observed feeding on red spider mites, but they occur only rarely in both sprayed and neglected orchards.

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SUMMARY.

A brief account is given of the life history and habits of the predators of the Fruit Tree Red Spider Mite which are not abundant in commercial orchards of South-eastern England at the present time. Twelve species of the family Miridae (Hemiptera-Heteroptera) are considered, and details given of their immature stages. Notes are given on species of the order Thysanoptera, and of the families Nabidae (Hemiptera-Heteroptera), Chrysopidae and Hemerobiidae (Neuroptera), and Syrphidae (Diptera), and of the Acarina.

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SPACING EXPERIMENTS ON VEGETABLES

VII. THE GROWTH AND YIELD OF GLOBE BEET, PARSNIPS AND CARROTS GROWN AT SEVERAL SPACINGS IN TWO ADJACENT FIELDS OF DIFFERENT FERTILITY

By **L. G. G. WARNE**
Botany Department, University of Manchester

In 1950 the opportunity arose to carry out spacing experiments, similar to those described previously (Warne, 1951b), in two adjacent fields differing greatly in their fertility. From these experiments it was hoped to obtain information about (i) desirable plant populations for root crops at different fertility levels, and (ii) the part fertility plays in restricting the growth of closely spaced plants. The two adjacent fields will be referred to by their ordnance survey numbers.

LOCATION OF EXPERIMENTS.

The field of high fertility is O.S. No. 133, and that of low fertility O.S. No. 131 (Cheshire, Knutsford Division XXV. 11. Parish of Lower Withington). The two fields are separated by a boundary which is probably "artificial" but of long standing. In both fields the soil is a heavy loam of glacial origin. Although precise information is not available, field No. 133, in which earlier experiments had been carried out, is known to have received frequent and heavy applications of organic and inorganic manures, and to have been frequently limed between 1936 and 1949. Over a like period field No. 131 has received little or no manure, apart from nitro-chalk and, prior to these experiments in 1950, had carried three successive crops of spring oats. The soils of the two fields were examined by the N.A.A.S. in the autumn of 1949 and a summarized report on them is as follows:

	Field No. 133	*Field No. 131*
pH	6·8	5·2
"Lime requirement" (cwt. $CaCO_3$ per acre)	—	45
"Available" phosphate	High	Very low
"Exchangeable" potash	Satisfactory	Very low

Field 131 received in the autumn of 1949 ground limestone at the rate of 2½ tons per acre and, after a winter ploughing, both fields received a spring dressing of 8 cwt. per acre of a mixture of three parts of superphosphate of lime, two parts of sulphate of ammonia and one part of sulphate of potash which was harrowed in. This fertilizer application was expected to produce moderate yields in field 131.

EXPERIMENTAL PROCEDURE.

The experiments to be described concern parsnips, carrots and globe beet* and the crops in the two fields received identical treatment. In each trial there were five treatments, each repeated five times in each field, giving a total of 50 plots of 54 sq. ft. for each crop. All three crops were sown with a hand-propelled Bean seed drill. They grew satisfactorily and exhibited no symptoms of mineral deficiency.

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* Similar experiments with long beet and onions were discarded. The long beet germinated unsatisfactorily and in field 131 only 12 per cent. of the onions produced "bulbs" and so no satisfactory comparison of yield in the two fields was possible.

Parsnips (var. Tender and True) were sown on 14th March, 1950 in rows 18 in. apart. Germination was good; expert labour was available for thinning and for this operation the men were provided with canes marked at appropriate intervals. Five nominal thinning distances were employed (2, 4, 6, 8 and 10 in.). The crop was harvested in October.

Carrots (var. Early Nantes) were sown on the 4th and 5th May, 1950 in rows 12 in. apart. Earlier experiments had suggested that in Field 133 not less than 290,000 carrots per acre were necessary for a maximum yield, but such a population is not easily obtained in rows 18 in. apart unless germination is good and regular. Variations in the plant populations were obtained by varying the setting of the drill, and no thinning was done. The chosen drill settings were expected to give plant densities of from about six per foot of row (approx. 260,000 plants per acre) to a maximum of 28 plants per foot of row. The plots were harvested in mid-September, 1950 (6th to 18th September).

Globe Beet were sown on 25th April, 1950 in rows 12 in. apart. Germination was moderate only. Five nominal thinning distances (1, 2, 4, 6 and 8 in.) were used and the plots were harvested late in August.

EXPERIMENTAL RESULTS.

The experimental results are most easily presented and discussed under the two main headings of (i) yield, and (ii) plant competition.

(i) *Yield.*

Parsnips. The results obtained with the parsnips are summarized in Table I. The populations obtained in both fields approximated closely to the "theoretical"

TABLE I.

Yield data for Parsnips.

	Field No.	Thinning distance					Mean	Signif. diff. P=0·05
		2 in.	4 in.	6 in.	8 in.	10 in.		
Population in thousands per acre ..	*	174	87	58	44	37	—	—
	133	156	82	59	43	39	76	—
	131	163	82	61	50	44	80	—
Total yield of roots: .. cwt. per acre ..	133	329	355	357	351	347	348	50
	131	228	232	221	196	194	214	27
Yield of "large" roots: .. cwt. per acre ..	133	95	307	353	337	330	284	47
	131	9·4	90	144	140	147	106	31
No. of "large" roots as per cent. of total no.	133	12·9	61·4	83·5	80·9	80·9	83	—
	131	1·6	23·5	49·5	53·9	59·6	60	—

* The theoretical population is shown in the first line of the Table.

populations for the five nominal thinning distances, with very small differences between the two fields. Total yields of roots averaged 348 cwt. per acre in field 133, and 214 cwt. per acre in field 131; in field 133 the yield was substantially the same for all thinning distances, but in field 131 the total yield fell when the thinning distance exceeded 6 in. (61,000 plants per acre).

The yield of large (2 in. diameter and over) roots in field 133 remained unchanged over the population range of 39,000 to 82,000 plants per acre, but fell when this number was exceeded; in field 131 it fell when the population exceeded 61,000 per acre. Practically, this is the most striking feature of the results—that the maximum number of plants permissible without loss of yield of large roots was less in the field of lower fertility.

Carrots. As shown in Table II, the populations in the two fields were again very similar, but in both fields there was a fall in total yield as the number of plants present decreased. In field 133 yields of large roots (over 1⅛ in. diameter) were at a maximum over the range of 270,000 to 714,000 plants per acre and in field 131 for the range 236,000 to 649,000. With more plants than this the yield of large roots fell in both fields.

Globe Beet. The populations obtained in the two fields differed somewhat, ranging from 64,000 to 154,000 plants per acre in field 131, and from 70,000 to 179,000 per acre in field 133, compared with the theoretical range of 65,000 to 532,000. The marked " deficiency " of plants at the close spacings accords with previous experience (Warne, 1951b and d, 1952). Total yields in field 131 (mean 159 cwt. per acre) were not significantly affected by the thinning distance, but the yield of

TABLE II.

Yield data for Carrots.

	Field No.	Setting of drill					Mean	Signif. diff. P=0·05
		13	11	9	7	6		
Population in thousands per acre ..	133	1237	975	714	402	270	720	—
	131	1237	960	649	394	236	684	—
Mean value equivalent to plants per foot of row	—	28·4	21·6	15·6	9·1	5·8	—	—
Total yield of roots: .. cwt. per acre ..	133	603	579	595	476	437	538	39
	131	475	455	427	374	294	405	45
Yield of " large " roots: .. cwt. per acre ..	133	270	348	413	414	393	368	47
	131	170	206	258	287	260	236	53
No. of " large " roots as per cent. of total..	133	20	31	44	60	77	—	—
	131	15	21	34	55	71	—	—
Percentage of " large " roots split ..	133	7·0	11·2	8·2	17·4	17·9	—	—
	131	13·5	18·2	15·0	25·4	27·3	—	—

large roots (over $1\frac{7}{8}$ in. diameter), which averaged 138 cwt. per acre for populations between 64,000 and 140,000 per acre, fell significantly to 104 cwt. when the population rose to 154,000 per acre. In field 133 the mean total yield for all distances was 409 cwt. per acre, but fell significantly to 377 cwt. when the population was only 70,000 per acre (slightly more than the minimum plant number obtained in field 131) ; the yield of large roots (mean 388 cwt. per acre) did not change significantly over the whole population range tested.

The data presented were obtained from two fields which received identical treatment in the year of the experiment and the results obtained cannot in any measure be attributed to differences in climate, skill of labour, management or husbandry. In the fertile field O.S. 133 the results obtained do not contradict the conclusions reached previously about desirable plant population for a fertile loam in Cheshire (parsnips 59,000 to 86,000, carrots not less than 290,000 and globe beet 120,000 to 140,000 and possibly more per acre). Comparing the yields in the two fields, no marked consistent effect of population change is evident but, with parsnips, increasing the population caused a decrease in the yield of large roots much sooner in the field of low fertility than in the more fertile one. With both parsnips and carrots there is evidence that, to produce maximum total yields of roots, a higher plant population was necessary in the field of low fertility, but this was not so for yields of large (saleable) roots. Although the total yields of the fields of high and low fertility differed so greatly, it is remarkable that the effects of altering the interplant distance were essentially the same in both. But, with parsnips and globe beet, increasing the plant population produced a harmful effect on the production of large roots, an effect which became evident at a wider spacing in the field of low fertility. This was not so, however, with carrots.

(ii) *Plant competition.*

From the yield data it is clear that, in both fields with all three crops, close spacing decreased the size of the plants, so that increases in the population did not cause proportionate increases in the total yield. In former papers (1951b, 1952) the dependance of root size on available space has been expressed in the form of a regression of available space on root weight. This procedure has again been followed with the results given below.

Regression of mean root weight, W (in oz.) on available space, A (in sq. in.). $W = x(A)^y$.

	Field 131	Field 133
Parsnips	$0{\cdot}12\ (A)^{0{\cdot}85}$	$0{\cdot}098\ (A)^{1{\cdot}0}$
Carrots	$0{\cdot}24\ (A)^{0{\cdot}79}$	$0{\cdot}23(A)^{0{\cdot}72}$
Globe beet ..	$0{\cdot}05\ (A)^{0{\cdot}98}$	$0{\cdot}13\ (A)^{0{\cdot}97}$

The extent of the dependance of size on available space is essentially the same in the two fields, although the yields differ considerably. This is perhaps best realized if, using these regressions, theoretical weights are calculated for roots grown at different spacings. Thus with parsnips, given 180 sq. in. per plant, root weight in field 133 is 17·6 oz. and, in field 131, 9·9 oz. and a reduction in the available area per plant to 72 sq. in. (i.e. by 60 per cent.) reduces root weight by 60 and 54 per cent. respectively. For carrots, with 24 sq. in. per plant, root weights are 2·96 oz. (field 133) and 2·27 oz. (field 131), and reducing the available area to 6 sq. in. per plant (i.e. by 75 per cent.) reduces root weight by 66·6 and 63·2 per cent. Weights of globe beet, allotted 96 sq. in. each, are 10·88 oz. (field 133) and 4·38 oz. (field 131) and a reduction in the available area per plant to 38·4 sq. in. (i.e. by 60 per cent.) reduces root weight by 58·4 per cent. (field 133) and 59·4 per cent. (field 131). This agreement between the results for the two fields is of special interest because other factors are known to affect the relation between available space and root weight. Thus, as the season progresses, the root weight for carrots and beet (Warne, 1951a) becomes increasingly dependent upon the area available to the plant (the yield becoming correspondingly less dependent upon the number of plants present). The regression also varies from year to year (Warne, 1952), but changes in the yield are not accompanied by consistent changes in the regression of available space on root weight.

This agreement between the results for the two fields makes it probable that the restricting effects of close spacing on growth are brought about by a factor or factors common to both fields and are not due to any fertility factor. This conclusion is confirmed by chemical data on the composition of the leaves of the experimental crops. Leaves were collected from all plots of globe beet (14th August) and carrots (21st August) and dried, and their contents of nitrogen (N), lime (CaO), potash (K_2O) and phosphate (P_2O_5) determined. The results obtained were subjected to an analysis of variance. The analytical data for leaves from the two fields differed considerably (Table III), but with neither crop was there any significant effect of spacing in either field.

TABLE III.

Chemical composition, as per cent. of dry weight, of beet and carrot leaves from fields 131 and 133. Mean values, standard errors in italics.

Crop	Field No.	N_2	CaO	K_2O	P_2O_5
Beet ..	131	3·81 *0·07*	4·61 *0·16*	2·43 *0·08*	0·50 *0·01*
	133	2·81 *0·04*	4·76 *0·11*	4·77 *0·10*	2·51 *0·01*
Carrots ..	131	3·52 *0·04*	3·10 *0·13*	1·66 *0·03*	0·53 *0·01*
	133	2·55 *0·06*	2·62 *0·07*	2·12 *0·07*	0·60 *0·01*

In neither field did the yield or chemical data provide evidence of any marked fertility gradient; but the beet responded more to the higher fertility of field 133, in both potash and phosphate, than did the carrots. This appears to agree with the results obtained by Wallace (1941a and b), and by Pickford (1944) in manurial experiments with these crops. In earlier experiments (Needham and Warne, 1952) it was suggested that, when nitrogen supplies were inadequate, close spacing resulted in competition for nitrogen and these chemical data apparently indicate that competitive effects might possibly be more severe in the highly fertile field. There is some inconclusive evidence that this was so for the parsnips, for which no chemical data are available but, if real, the effect was slight and is not supported by the data for the other two crops. The similarity of these spacing effects in the two fields suggests that none of the factors which constituted the " fertility difference " between the fields could account for the restrictive effects of close spacing on plant growth.

Throughout the season when inter-plant competition operated, rainfall (at Ringway Airport) was abundant. In only one week after 9th June was the rainfall less than 0·40 in. and the minimum rainfall recorded in any seven-day period after 7th July was 0·47 in. (following a week with 0·86 in. of rain), and it is unlikely that a water deficiency could account for the results obtained. Light is unlikely to have been the major factor in inter-plant competition. Inspection of the plots showed a much less luxurious growth of foliage in field 131 than in field 133. This is illustrated by the beet only, for in field 131 the mean weight of tops per plant at harvest was 1·31 oz. and, in field 133, 1·86 oz. Hence we should have expected the amount of mutual shading of closely spaced plants in the two fields to differ considerably and, therefore, the regressions of available area on root size to differ, if this were an important factor in restricting growth. The regressions, however, are almost identical. Thus, of the factors common to both fields, light and water supply appeared not to be the operative factors in determining the effects of close spacing on growth. This experiment therefore confirms the conclusions reached from combined manurial and spacing experiments on beet and shallots (Warne, 1951c and d, and Needham and Warne, 1952), namely, that competition between closely spaced crop plants is not entirely competition for water, light or the major nutrients estimated.

SUMMARY.

1. Spacing experiments on globe beet, parsnips and carrots were carried out in two adjacent fields differing in their fertility. The three crops responded differently to the different fertility level both in yield and chemical composition of the foliage.

2. To produce maximum total yields of roots, higher populations of carrots and parsnips were necessary in the field of low fertility than in the field of high fertility, but this was not so for yields of " large " (saleable) roots ; although, with parsnips and globe beet, fewer plants were permissible in the former field for maximum yields of large roots. No such effect was evident for carrots, within the population ranges tested.

3. Close spacing of the carrots tended to decrease the incidence of splitting.

4. Root weight was equally dependent on the area available for growth in the two fields and no effect of spacing on the contents of nitrogen, lime, potash or phosphate in the foliage of the beet or carrots was found in either field.

5. These observations of the spacing effects in the two fields tended to confirm a previously expressed view that the effects of close spacing in restricting growth cannot be explained solely in terms of competition for light, water or the major nutrient elements.

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STOCK AND SCION INVESTIGATIONS

VII. A NURSERY TRIAL WITH CLONAL PEAR ROOTSTOCKS

By L. A. THOMAS*

Commonwealth Scientific and Industrial Research Organization, Division of Plant Industry

THE lack of uniformity observed in size of trees on seedling rootstocks in pear orchards at Stanthorpe prompted an investigation into the possibility of achieving more even plantations by using the vegetatively reproduced pear stocks already tested at East Malling (Hatton, 1933).

MATERIALS AND METHODS.

Rootstocks, Malling Nos. B1, C2, C7, D3 and D4, which had been found to transplant more readily than others, were introduced from East Malling, propagated at Stanthorpe, and budded to Williams' Bon Chrétien pear. Sufficient trees for the trial were ready in 1941, and those on four of these rootstocks were planted out in a nursery trial together with Williams' pear trees on a clonal selection of *Pyrus Calleryana* obtained from a nursery.

The trial was planned in randomized blocks with thirty trees on each rootstock, except C7, on which only twenty-five trees were available. The rows of trees were 6 ft. apart, with the trees spaced 5 ft. apart in the rows.

On two sides of the trial there were guard row trees of Williams' on the above stocks and, on the other two sides, Packham's Triumph pear on Malling Nos. B1 and D3 as pollenizers.

The trees were trained to a single stem. The heavy laterals were cut back each winter to form fruiting arms or sub-leaders ; the lighter laterals, up to 15 in. in length, were left unpruned to bear fruit at the terminal buds and, in their second year, pruned back to convenient spurs.

Zinc sulphate sprays were applied annually as a precaution against Little Leaf ; copper sulphate at the rate of 100 lb. per acre was applied in 1943 against Summer Dieback and borax at 5 lb. per 100 gallons spray mixture from 1943, in which year boron deficiency symptoms were observed (Thomas, 1944).

Measurements were made of the length of annual new wood growth from 1941 to 1946 ; of the girth of the trunk at a fixed height, from 1945 to 1950, and of the weight and count of fruit borne.

RESULTS.

Nursery experiences.

The proportion of rooted shoots obtained from the layer beds, varied from 30 to 40 per cent. each year.

Rootstock C2 developed Crown Gall† the first season, when planted in virgin ground, with galls up to 2 in. in diameter. No further use was made of this rootstock.

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* An officer of the Division of Plant Industry located at Stanthorpe, Queensland.

† No isolation of the pathogen was made. Galls due to *Bacterium tumefaciens* are common enough here to be recognized.

When D4 rootstocks from the layer beds were lined out for budding, transplanting losses were about 30 per cent. Further, after the one-year-old trees were planted out, eight of the twenty-four experimental trees and one of the ten guard-row trees died. These were replaced successfully the following year. All trees on the other rootstocks transplanted satisfactorily.

Hatton (1933) reports similar experiences with these East Malling pear rootstocks and with pear seedlings, with between 30 and 68 per cent. of bedded rootstocks surviving after transplanting, according to the variety.

Annual wood growth.

As shown in Table I, trees on *P. Calleryana* made the most annual wood growth, and trees on D4 the least.

In the spring of 1945, all trees on stock C7, and no others, were affected with "sour sap" due to a late frost. Two trees were killed almost to ground level; many branches and laterals were killed back to the trunk. It is therefore probable that, without this check, trees on C7 would have shown more growth in 1946 than trees on B1.

TABLE I.

Average wood growth, 1941-46, and coefficients of variability (V) in wood growth, 1946, on different rootstocks.

Stock	Wood growth (m.)			Intra-plot variation	
	1941	1946	1941-46	V	Variance of V
P. Calleryana ..	1·4	53·4	150	32·6	21·4
D3	2·3	38·1	116	20·7	7·7
B1	2·4	26·2	93	24·1	10·8
C7	1·0	23·4	75	21·8	11·3
D4	1·7	19·8	61	39·8	34·8
Minimum difference for significance					
P = ·05		10·1	25·7		
P = ·01		14·0	35·4		

As could be expected from the poor establishment after transplanting, trees on D4 exhibit a greater coefficient of variability than all others.

Growth as measured by girth of trunk.

As annual wood growth could not be measured after 1946, girth of trunk at a fixed height (4 in. above the unions) was measured from 1945 onwards until 1950. The data are shown in Table II.

The largest trees by this measurement were still those on *P. calleryana* stocks, followed by those on D3. By 1950, trees on B1 had somewhat slimmer trunks than on D4 and C7, the difference between the three being insignificant, reversing the position shown by the wood growth to 1946 and the girth in 1945, when B1 was significantly larger than D4, C7 being intermediate.

TABLE II.

Average trunk girth in 1945 and in 1950 on different rootstocks.

Stock.	1945 cm.	1950 cm.
P. Calleryana	15·6	24·9
D3	14·7	22·7
B1	12·9	18·4
C7	12·6	19·1
D4	11·7	19·1
Minimum difference for significance *P*=0·5	1·0	1·3

Cropping.

The average total crop per tree between 1946 and 1950 is shown in Table III. Most of the fruit was borne in the years 1948 and 1950, spring frost having destroyed the crop after fruit set in 1949.

TABLE III.

Average total crop in lb. per tree 1946-50.

Stock	lb.
D3	44·6
C7	26·8
P. Calleryana	23·3
D4	20·0
B1	6·0

Trees on D3 have consistently borne the heaviest crop, while the largest sized trees on *P. Calleryana* cropped less heavily than those on C7, which are about half their size. Rootstock B1 stands apart in its poor cropping performance.

Comparison of growth with proportion of bark in roots.

Beakbane *et al.* (1941), determined the percentage of bark in the roots of different apple stocks and found a negative correlation between vigour, as expressed by wood growth of a scion, and root structure.

TABLE IV.

Comparison of percentage bark in three-year-old roots and trunk girth of ten-year-old Williams' Bon Chrétien on different rootstocks.

Rootstock	Percentage bark in roots	Trunk girth 1950 (cm.)
Williams' Bon Chrétien (on own roots) ..	43	no data
,, ,, ,, on B1	43	18·4
,, ,, ,, on *P. Calleryana*	59	24·9
,, ,, ,, on C7	98	19·1
,, ,, ,, on D3	104	22·7

The same method was used by the writer to determine the percentage of bark in the root in this series of pear stocks, using three-year-old roots. From the results in Table IV, it is seen that there is no correlation between vigour of scion, as expressed by trunk girth in 1950, and percentage of bark for these particular combinations of rootstock and scion.

DISCUSSION.

The difficulties in making generalizations for the behaviour of different scion varieties upon clonal pear rootstocks will be apparent when comparing the results obtained with Williams' Bon Chrétien described above, with those for Dr. Jules Guyot in England (Hatton, 1933) and Kieffer in Canada (Upshall and Dickson, 1949).

Rootstock D3 produced trees of medium vigour with Dr. Jules Guyot, dwarfed trees with Kieffer and vigorous trees with Williams' Bon Chrétien. Rootstock B1 produced small crops with Dr. Jules Guyot, large crops with Kieffer and small crops with Williams'.

With pear trees, it seems that partial compatibilities of any stock-scion combination have a large effect upon the vigour and cropping habit of the scion.

SUMMARY.

A ten year trial with Williams' Bon Chrétien pears on clonal pear rootstocks showed that the greatest scion growth, as measured by length of annual shoot growth and by girth of trunk, occurred with rootstocks *Pyrus Calleryana* and East Malling No. D3.

Largest total crops were borne by trees on East Malling No. D3. Other rootstocks under trial were East Malling Nos. B1, C2, C7 and D4. Rootstock B1 suckers badly, D4 is difficult to transplant, C2 appears susceptible to Crown Gall and C7 produced small trees which suffered frost damage.

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STOCK AND SCION INVESTIGATIONS

VIII. A PRUNING AND ROOTSTOCK TRIAL WITH APPLE TREES

By L. A. THOMAS*

Commonwealth Scientific and Industrial Research Organization, Division of Plant Industry

It is recognized that the pruning of young apple trees, to produce the desired shape and stature, delays cropping. In Australia, where the semi-dwarfing Northern Spy rootstock is widely used, it has been the object of many orchardists to keep the tree in a vegetative state until such time as a framework of sufficient size is built, by pruning leaders and laterals severely and by removing blossoms or young fruits.

After the publication by Wickens (1938) of his experiences with trees with unpruned leaders, when he showed that, despite early cropping, vigorous growth could be maintained in young apple trees and a suitable framework of limbs developed, it was decided to include a series of trees trained by his method in a combined rootstock and pruning trial.

As vigorously growing young trees seemed necessary for the success of Wickens' method, the most vigorous clonal rootstock available, Malling No. XII, a local vigorous clonal rootstock Essfour (S4) (Thomas, 1947) and Ivory's Double Vigour, obtained from New Zealand, were used.

MATERIALS AND METHODS.

One-year-old Jonathan whips on the three rootstocks were planted in 1939 at 20 ft. apart. There were nineteen plots arranged at random each containing two Jonathan trees on each of the three rootstocks. To ensure adequate pollination, one tree in every nine was a Granny Smith on Essfour rootstock, planted symmetrically so that every Jonathan tree was no more than 20 ft. away from a pollenizer.

The external guard trees were Granny Smith on Essfour and Ivory's Double Vigour rootstocks.

Three treatments were applied to the Jonathan trees: six plots received hard pruning, six medium pruning and seven plots were treated according to Wickens' method. In the hard-pruned trees, three-quarters of the length of the annual leader growth was removed each winter and all laterals were cut back to five buds, thus building up a system of spurs and short laterals. Sub-leaders were developed slowly, as at least three-quarters of the extension growth was pruned away.

In the medium-pruned trees, two-thirds of the length of new leader growth was removed each year ; laterals up to 15 in. long were left unpruned until their second year, when they were pruned back to convenient fruit buds or spurs ; all laterals longer than 15 in. were cut back to five buds. Sub-leaders were developed with not more than two-thirds of the shoot growth removed.

Under Wickens' method (see also Wickens, 1939) the leaders are allowed to grow unchecked from the time of planting, nicking above buds is practised to force lateral growths at desired points, and chosen laterals are left to grow on, unpruned, to form further leaders or sub-leaders. The centre of the tree is kept open by suppressing any vigorous upright growths. The main limbs are spread when young, to form a broad-based tree. For the first three years, blossoms or young fruits are removed from the tips of the leaders and the bunched shoots at leader tips thinned out to one.

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* An officer of the Division of Plant Industry located at Stanthorpe, Queensland.

In this trial, Wickens' method was slightly modified. No fruit was allowed to develop at the leader tips in any year ; from the sixth year onward, the more vigorous leaders were pruned and, in the later years, all leaders were pruned.

The twelve Granny Smith trees planted as pollenizers within the trial were pruned by Wickens' method, while the external guard trees on Essfour and Ivory's Double Vigour rootstocks were hard pruned.

Instead of the " maypole " support for the limbs of the Wickens' trained trees, a single rope around the tree, at about 6 ft. from the ground, has kept the trees in shape.

All fruit clusters were thinned to two fruits. Measurements made were girth (cm.) of trunk at a fixed height above the union, height and spread (in feet) of tree, number and weight of fruits borne.

Results.

Jonathan.

Growth. The data for growth, as measured by girth of trunk in 1950, are presented in Table I and Fig. 1.

Table I.

Girth in cm. of eleven-year-planted Jonathan on three rootstocks under the three systems of pruning.

Pruning treatment	M.XII	Essfour	Ivory's Double Vigour
Hard	44·8	43·8	33·6
Medium	44·5	44·6	32·1
Wickens' method	47·7	46·1	32·5

The size of the trees on Ivory's Double Vigour stock was considerably less than those on Essfour or Malling XII.

The differences in trunk girth between trees receiving the three methods of pruning were not significant for any of the three rootstocks.

The sizes of the trees as measured by height (ft.) and spread (ft.) are compared in Table II as the product of these measurements.

This measurement of growth confirms the tendency shown in Table I, for the largest trees for all treatments to be those pruned by Wickens' method on rootstocks Malling No. XII and Essfour. By this measurement, the Wickens'-pruned trees on Ivory's Double Vigour stock are also larger than those pruned by the other two methods.

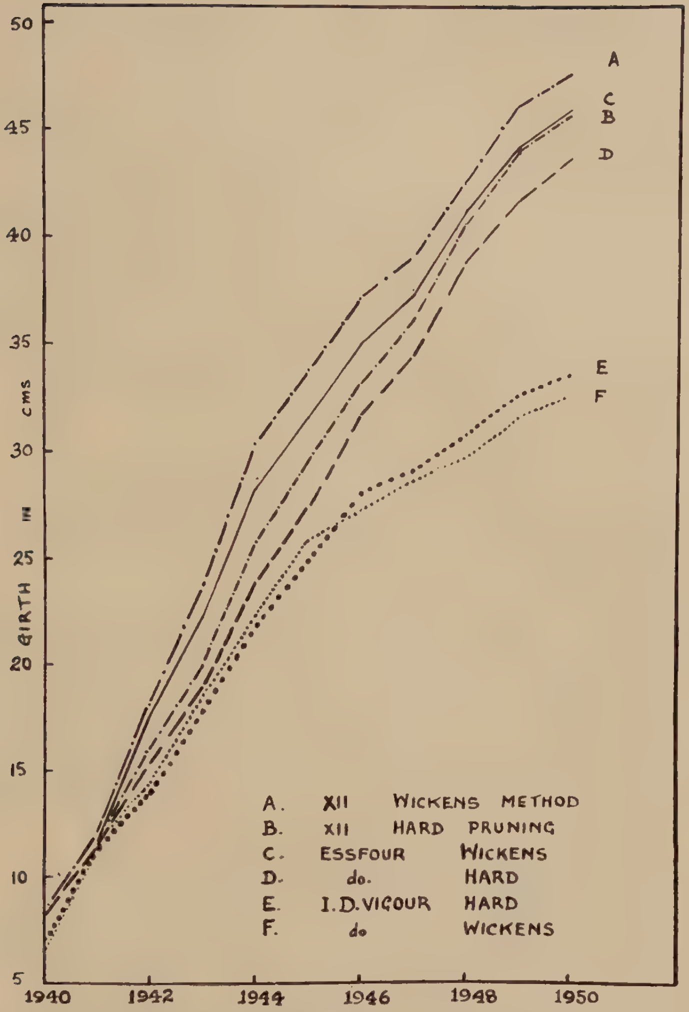

FIG. I.

Trunk girth of Jonathan on three rootstocks with two methods of pruning 1940-50.

TABLE II.

Comparative size of Jonathan on three rootstocks under three pruning treatments as shown by the product of the height and spread of the trees, measured in feet.

Treatment	M.XII	Essfour	Ivory's Double Vigour
Hard pruning	89	85	67
Medium pruning	97	95	67
Wickens' method	136	130	88
Minimum difference for significance P = ·05 ..	16	16	16

Cropping. The crops of the Jonathan trees in the fifth and eleventh years after planting and for the whole period are shown in Table III.

TABLE III.

Average crop in lb. per tree of Jonathan on three rootstocks and under three pruning treatments.

Rootstock	M.XII			Essfour			Ivory's Double Vigour		
Treatment	1944	1950	Total	1944	1950	Total	1944	1950	Total
Hard pruning	1·5	254	451	2·5	203	357	3·6	162	356
Medium pruning	10·0	253	500	12·7	208	419	15·7	157	382
Wickens' method	16·5	311	778	21·6	308	686	18·6	200	520
Minimum difference for significance P = ·05 ..	—	—	101	—	—	101	—	—	101

On all rootstocks the largest annual crops have matured on trees pruned by Wickens' method.

The difference in the total weight of crops between the hard- and medium-pruned trees is largely due to the fruit borne on the long unpruned laterals during the early cropping years of the medium-pruned trees; these differences have disappeared by 1950, when cropping for both treatments is approximately the same.

Size of fruit. In order to discover whether the rootstocks used or the pruning treatments applied had any effect on the average weight of the fruits, records were made of the number and total weight of fruits on each tree each season (Table IV).

TABLE IV.

Yearly fruit count and average number of fruits to the pound.

Rootstock	Year	Hard pruning		Medium pruning		Wickens' method	
		Count	Average per 1 lb.	Count	Average per 1 lb.	Count	Average per 1 lb.
M.XII	1946	660	3·4	692	3·2	3754	3·7
	1947	2673	3·9	3775	4·1	8346	5·1
	1948	4452	3·1	5052	3·1	11314	3·4
	1950	10200	3·3	10461	3·4	16632	3·8
Essfour	1946	347	3·1	508	2·9	2871	3·4
	1947	2369	3·5	3674	3·6	7548	4·4
	1948	2978	3·0	3444	3·1	7389	3·4
	1950	7233	3·0	7455	3·0	13099	3·5
Ivory's Double Vigour	1946	1008	2·9	1387	2·9	4025	3·5
	1947	2336	3·5	2681	3·2	4656	4·6
	1948	3460	3·0	3829	3·1	6348	3·5
	1950	6502	3·3	6364	3·4	8910	3·7

Note: There was no crop in 1949 owing to frost damage.

It will be seen that the fruits were smaller on the Wickens' pruned trees on all rootstocks. This is probably related to the heavy crops borne by these trees but such fruits were not too small for commerce.

The fruits from trees on M. XII were smaller than those from trees on the other two stocks with all pruning treatments. Observations made show that trees on M. XII tend to produce a number of very small fruits among normal-sized ones, both with Jonathan and Granny Smith as scions.

The smallest fruits were matured in 1947 on all rootstocks and with all treatments, except the medium pruned trees on Ivory's Double Vigour, probably because of the period of dry weather before harvesting.

Granny Smith.

Growth. Table V summarizes the growth as measured by girth of trunk and by the product of height × spread of tree.

TABLE V.

Growth measurements of Granny Smith.

Rootstock and treatment	Girth (cm.)	Height (ft.) by Spread (ft.)
(*a*) Ivory's Double Vigour hard pruned	31·5	51·3
(*b*) Essfour hard pruned	41·9	73·0
(*c*) Essfour Wickens' method	46·3	119·6
Significance of difference		
between (*a*) and (*b*)	P = ·001	P = ·001
between (*b*) and (*c*) ..	P = ·05	P = ·001

With Granny Smith on Essfour rootstock, it is again evident that Wickens' method of pruning has produced the larger trees ; Ivory's Double Vigour rootstock is again not as vigorous as Essfour.

Cropping. The total weight of crop matured on the Granny Smith trees from 1945-50, is shown in Table VI. This variety set its first small crop one year later than Jonathan. The 1949 crop was destroyed by frost. The difference in

TABLE VI.

Average crops in lb. per tree, 1945 to 1950, of Granny Smith.

External guard trees hard pruned		Internal pollenizers Wickens' method
Ivory's Double Vigour	Essfour	Essfour
322	291	731

Note : There was no crop in 1949 owing to frost damage.

crop weight for the two pruning methods on the trees on Essfour rootstocks is more striking with Granny Smith than with Jonathan, being approximately 2½ times greater for Granny Smith and twice for Jonathan.

Over the whole of this period, unlike Jonathan, the smaller Granny Smith trees on Ivory's Double Vigour carried rather heavier crops than did the larger trees on Essfour. But in the last year, 1950, the order was reversed.

The average number of fruits to 1 lb. weight for the total crop was 2·30 for hard-pruned trees on Ivory's Double Vigour, 2·21 for hard-pruned trees on Essfour and 2·49 for Wickens'-pruned trees on Essfour stock.

DISCUSSION.

The usefulness of Wickens' method in orchards needs consideration in light of the fact that, as Wickens (1938, p. 377) has pointed out, it takes longer to deflower the leading shoots and thin out the tufted shoots at the tips of the leaders, than to carry out normal winter pruning. But as the method both produces a large tree and gives an early financial return on invested capital through early and large crops, it would appear to be a suitable pruning method for those establishing a young orchard on limited capital.

In choosing a rootstock for trees to be treated by Wickens' method, it appears that a vigorous stock is desirable, at least in such a district as Stanthorpe.

SUMMARY.

Jonathan apple trees on the clonal rootstocks Malling No. XII, Essfour and Ivory's Double Vigour were given three pruning treatments for eleven years from their planting in 1939. Trees pruned by Wickens' method (unpruned leader trees) grew larger and bore heavier crops than did those that were hard- or medium-pruned. Confirmatory results were obtained with Granny Smith on Essfour rootstock.

Ivory's Double Vigour produced a much less vigorous tree with Jonathan and Granny Smith than did Essfour or Malling No. XII rootstocks.

ACKNOWLEDGMENTS.

My thanks are given to Mr. G. A. McIntyre of C.S.I.R.O. for carrying out the statistical analysis of the data.

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LIME DIEBACK IN THE GOLD COAST, A VIRUS DISEASE OF THE LIME, *CITRUS AURANTIFOLIA* (CHRISTMANN) SWINGLE

By W. A. HUGHES* and C. A. LISTER†

THE Lime, *Citrus aurantifolia* (Christmann) Swingle is common throughout the Gold Coast but only within 25 miles north of Cape Coast is it grown on a commercial scale. The individual plantations are from one to three acres in extent and are owned by the peasant farmers who sell the crop to a firm of cordial manufacturers for export.

The lime die-back disease has probably been present for many years, the first signs of serious trouble having been noticed in 1938. By 1947, many trees were dead and it was almost impossible to grow limes from seed in the open.

Shepherd (1945) reported a vein-flecking in the diseased limes which will be described later. He investigated the role of *Ganoderma lucidum* Leyss. ex Fr. and a species of *Trametes* common on diseased trees, and concluded that these fungi were not responsible for the decline.

Fennah (1947) made a rapid survey of the lime area and suggested that a virus might be responsible but considered that the nutritional status of the limes should first be investigated.

Lister (1947, 1948) showed that the decline was not caused by malnutrition, fungi or bacteria. He established that it was due to a virus and commenced the investigation into possible alternative hosts.

SYMPTOMS.

The disease has been observed in limes of all ages. The leaf veins become clear and translucent when viewed by transmitted light. The clearing may be patchy, producing a " vein flecking ", or the cleared veins may form a network covering the whole leaf. The symptoms are most apparent in the young leaf and may disappear as the leaf hardens. A corky enation of the veins on the upper side of the leaf is often observed on experimental plants but is rare in the field. This condition has been named " corky vein ".

When the bark is peeled off the branches, brown pits and longitudinal streaks are sometimes seen in the surface of the xylem. Microscopical examination shows that the pits are caused by gumming in the xylem and, to a lesser extent, in the phloem. The gumming appears to start in the cambium, which produces large thin-walled cells which become filled with gum and ultimately degenerate, leaving a pocket of gum. Isolated cells are present, floating in the gum. Intercellular gumming may occur and scattered xylem vessels may be blocked by plugs of gum.

In the later stages of the disease, the branches usually die back, either from the crown or, more often, on one side, producing the one-sided die-back which is common in the field. A sector of the bark often dies, producing a strip of dead tissue which may be traced from a dead root, along one side of a main branch to a dead twig at its distal end. This necrotic bark symptom has been called " sectorial die-back ".

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* Now at the Edinburgh and East of Scotland College of Agriculture.

† Now at the Shell Agricultural Experiment Station, Sittingbourne, Kent.

The root hairs of diseased trees die and are not replaced. This is followed by the gradual death of the roots and, ultimately, of the whole tree.

STARCH RELATIONSHIPS.

Diseased seedling limes show an irregular distribution of starch similar to that described by Bitancourt (1944) and Fawcett (1945, 1946). Fifty young seedling limes were split longitudinally along the stem and main root, and a 2 per cent. aqueous solution of iodine potassium iodide washed over the exposed wood. The healthy seedlings showed a uniform distribution of starch throughout the stem, nearly all the diseased plants being devoid of starch. Leaves from these seedlings were boiled in water for fifteen minutes and then stained in the iodine potassium iodide. In the leaves from the healthy seedlings, starch was uniformly distributed from the lamina through the petiole into the branch. Leaves from diseased seedlings showed a heavy deposit of starch in the petiole, which ended in the vicinity of the abscission layer, with no starch in the stem. Three healthy and three diseased seedlings were kept in the dark. Daily tests showed that all starch disappeared from the leaves of the healthy plants after fourteen days but traces of starch remained in the leaves of the diseased plants.

SAP INOCULATION.

Two attempts were made to transmit the disease by sap inoculation. In the first, the sap was filtered through filter paper and was rubbed on the leaves of ten healthy seedlings with a strip of fine glass paper.

In the second, infected lime leaves were passed through a meat mincer, the pulp was squeezed through a piece of boiled muslin, and the sap was filtered through filter paper. Ten healthy lime seedlings were inoculated, using powder from a " carborundum " razor-hone as an abrasive. The inoculated leaves were washed with distilled water immediately after inoculation. Controls were ten healthy lime seedlings in each experiment. No symptoms were seen on any of the plants.

GRAFT TRANSMISSION.

Seedling limes grown in the open were used in most of the experiments until an insectary was available, with the result that chance infection occurred in some of the controls.

During January, 1948, fifty-eight seedlings were grafted with twigs from a lime showing veinal symptoms and crown die-back ; another fifty were grafted from a lime showing veinal symptoms and a dwarfed habit. Results of both experiments are given in Table I.

These two experiments show that the disease and the dwarfed habit are transmissible.

VIRUS STRAINS.

The experiments indicated that there are two strains of the disease. In the field, the commoner set of symptoms shows clearing and flecking of the leaf veins which may be followed by the sectorial die-back of the bark and by a die-back of the young twigs. This has been named the " die-back " strain. The other set

TABLE I.

Transmission of various diseased conditions by grafting.

January, 1948.

	Number of plants in each test	Number of plants showing transmission of:			Controls	
		Vein-flecking	Die-back	Dwarfing	No.	Disease symptoms
Experiment 1 ..	58	58	6	Nil	60	Nil
Experiment 2 ..	50	50	Nil	50	50	Nil

includes the leaf vein-clearing and flecking, but die-back of the bark and twigs is less common. The leaves are reduced in size, and the twigs shortened, producing a stunted habit. This has been called the " little leaf " strain. The word " strain " is used loosely as it is not yet known whether one or more viruses are involved.

ALTERNATIVE HOST EXPERIMENTS.

Rootstocks.

Bark from *stocks* carrying infected limes was grafted to healthy lime seedlings during April, 1948. The controls were similar lime seedlings grafted with bark from young seedlings of sour orange, rough lemon, lake and Sampson tangelo. The results obtained by the end of June, 1948, are given in Table II.

TABLE II.

Results of veneer grafting healthy lime seedlings with bark from stocks bearing diseased lime scions.

April, 1948.

Variety of stock used	Test plants		Controls	
	No.	No. showing vein-clearing	No.	No. showing vein-clearing
Sour orange	10	10	10	Nil
Rough lemon	10	10	10	1
Lake tangelo	10	9	10	Nil
Sampson tangelo ..	10	9	10	Nil

It is evident that sour orange, rough lemon, lake and Sampson tangelo, when used as rootstocks for infected lime scions, can carry the virus of lime die-back.

Sweet Citrus.

At Asuansi, varieties of sweet citrus budded on sour orange stocks suffer from a condition resembling tristeza or quick decline, as described by Klotz and Fawcett (1948).

Shoots from the varieties listed in Table III, were grafted on healthy lime seedlings during January, 1949. Similar varieties, budded on rough lemon stocks, were also used. Controls were ungrafted healthy seedling limes as no healthy sweet citrus was available to graft the controls. The results are given in Table III.

In view of the similarity of the symptoms in the indicator lime plants, it is a reasonable assumption that the sweet citrus listed in Table III were carrying the lime die-back virus.

TABLE III.

Results of side-shoot grafting of healthy lime seedlings with Sweet Citrus believed to be suffering from Tristeza.

January, 1949.

Variety	Original rootstock	No. of test plants	No. showing vein-clearing	No. showing corky vein
Mediterranean sweet orange	Sour orange	11	5	Nil
Mediterranean sweet orange	Rough lemon	8	7	Nil
Washington navel orange	Sour orange	11	11	Nil
Washington navel orange	Rough lemon	15	7	3
Satsuma	Rough lemon	15	4	Nil
Tangerine	Sour orange	22	4	Nil
Tangerine	Rough lemon	15	11	3
Marsh grapefruit	Sour orange	17	14	2
Marsh grapefruit	Rough lemon	18	11	Nil
	CONTROLS.			
Seedling limes	—	63	2	1

Other alternative hosts.

During 1948, not less than five seedlings of each of nine species of *Rutaceae* were grafted with scions from diseased limes. After grafting, the plants were allowed to grow for varying periods, then tissue from them was grafted back to healthy lime seedlings as indicators for the lime die-back virus. Results from the indicator plants are given in Table IV.

TABLE IV.

Alternative hosts. Results of back grafts on indicator lime seedlings.

Host	Test plants		Controls	
	showing vein-clearing	showing corky vein	showing vein-clearing	showing corky vein
Rough lemon	9/12	0/0	0/10	0/0
Lemon	7/11	0/0	0/10	0/0
Sour orange	9/11	0/0	0/10	0/0
Trinidad wild grapefruit	14/14	0/0	3/7	0/0
Syrian orange	10/10	0/0	3/10	0/0
Citron	9/10	0/0	2/10	0/0
Aeglopsis Chevalièri Swingle	9/10	0/0	0/10	0/0
Afraegle paniculata (Schum.) Engl.	18/20	0/10	2/20	0/10
Clausena anisata (Willd.) Hook.	7/10	0/0	4/10	0/0

The rough lemon, lemon, Trinidad wild grapefruit, Syrian orange and *Clausena anisata* did not display symptoms, although the back grafts showed that these plants carried the lime virus.

The growth of the sour orange was retarded and the leaves became chlorotic after being grafted with tissue from diseased limes. The sour orange remained alive for two years, although it did not make any growth between grafting and being discarded.

Four out of six of the grafted citrons developed a discontinuous yellow clearing of the leaf veins. The symptoms were confined to leaves which had hardened off; they faded gradually and disappeared after one year. The affected plants grew more slowly than the two apparently healthy citrons which had remained free of symptoms and which were not back-grafted to lime seedlings.

Twelve seedlings of *Aeglopsis Chevalièri* were grafted; two months later all developed a diffuse mottle on the young leaves. Succeeding leaves were free from symptoms but, after a further six months, four plants produced distorted leaves with cleared veins whilst another plant showed "corky vein" and retarded growth. It is concluded that *Aeglopsis Chevalièri* displays vein-clearing and leaf distortion when infected with the lime die-back virus, but the significance of the early leaf mottle is not known.

Six seedlings of *Afraegle paniculata* were grafted and, six months later, four produced leaves with a continuous clearing of the leaf veins but there was no distortion of the leaves. In addition, two of these four showed the "corky vein" symptom on their lower leaves. This was not transmitted in the back-grafts to lime seedlings.

Ten seedlings of *Citropsis articulata* Swingle were grafted with twigs from diseased limes, and all developed a severe leaf chlorosis. Three months after being grafted, all the plants shed their leaves and died.

VECTOR EXPERIMENTS.

Menghini (1947) reported *Aphis citricidus* (Kirk) to be a vector of tristeza. The aphid is a common pest of limes on the Gold Coast and was tested as a vector of lime die-back.

Materials and methods.

Each plant was caged separately in a cellophane sleeve closed at the top with muslin and sealed at the base, with adhesive tape, to a bamboo pot.

The source plants were lime seedlings, about fifteen months old, which had been grafted with the "little leaf" strain of the virus. In the first experiment, test plants were lime seedlings transplanted from a nursery but, in the second, seeds were germinated in petri dishes and the seedlings were kept under insect-proof conditions throughout.

First transmission by Aphis citricidus.

Two of the source plants were used for the short feeding time of five and ten minutes and another two for the long feeding times.

A bombardment technique was used to infect the test plants each of which received six groups of insects successively, as shown in Table V.

Each test plant thus received fifty-two aphids which were allowed to feed for

TABLE V.

Feeding times of Aphis citricidus *in bombardment infection experiments. 14th to 16th June, 1948.*

Time	Number of aphids transferred	Pre-infection starvation period
5 mins.	6	3 hrs.
10 mins.	6	3 hrs.
1 hr.	10	nil.
3 hrs.	10	nil.
6 hrs.	10	nil.
24 hrs.	10	nil.

ten days from the date of the last transfer. Growth was slow and the cages were removed twenty days later.

Leaf symptoms, consisting of vein-clearing, appeared on six plants thirty-eight days from the date of the last insect transfer. The vein-clearing was more intense and generally distributed than that observed in the field.

Later, the symptoms decreased in intensity from the fairly uniform vein-clearing to a marked vein-flecking, with cleared and uncleared lengths along the vein when viewed by transmitted light, and ultimately some plants produced symptomless leaves. After six months, two of the plants showed the reduced leaf size and dwarfing characteristic of the " little leaf " strain, whilst the other four infected plants had grown vigorously.

Ten healthy lime seedlings used as controls showed no symptoms.

Second transmission by Aphis citricidus.

Groups of test limes raised under insect-proof conditions were then treated with aphids which had been allowed to feed on the source plants for differing periods.

The controls each received ten aphids direct from the rough lemons in the nursery.

The infection feeding times and results are given in Table VI, the numbers of test seedlings being those remaining alive at the end of the experiment. A pre-infection starvation period of three hours was given to the insects used in Experiment

TABLE VI.

Transmission of infection by Aphis citricidus *after various feeding times.*

Experiment number	Feeding time	No. of test seedlings. Ten insects each	Infected test seedlings	No. of controls. Ten insects each	Infected controls
1	10 mins.	9	1	10	1
2	1 hr.	7	4	9	nil.
3	3 hrs.	9	4	10	1
4	6 hrs.	10	6	9	4
5	12 hrs.	10	7	10	3
6	24 hrs.	10	8	9	1
7	24 hrs.	19	18	19	5

I, the insects in the remaining experiments being transferred direct from the rough lemons to the source plants.

The symptoms in both test and control plants appeared approximately one month after the transfers and resembled those described.

Transmission by mealybugs.

Mealybugs, identified as *Ferrisia virgata* (Cockerell), were found on a lime and were tested as a vector, this mealybug having been described as a vector of swollen shoot by Posnette (1947).

Materials and methods.

Lime seeds were germinated in petri dishes lined with moist filter paper. After germination, the seedlings were transplanted into specimen tubes partially filled with sterilized sand. Test feeding was done in these tubes, the mouths of which were closed by squares of muslin secured by rubber bands. The source plants were the same as in the aphid experiments.

In the first experiment, mealybugs were allowed to feed on the source plant for thirty hours, and then transferred to each of eight lime seedlings, after twelve days the seedlings were knocked out of the tubes, the mealybugs washed off with 50 per cent. alcohol, and the seedlings potted into cigarette tins of sterilized soil in an insectary.

In the second experiment similar source and test plants were used. Each test plant received twenty mealybugs, ten of which had been fed on the source plant for twenty-four hours and ten for three hours.

Controls for both experiments were similar lime seedlings which received no insects. Results are given in Table VII.

TABLE VII.

Transmission of infection by mealybug (Ferrisia virgata (*Cockerell*)).

Experiment number	Feeding times	No. of test plants	Infected test plants	No. of controls	Infected controls
1 ..	30 hrs.	8	6	8	1
2 ..	24 and 3 hrs.	10	9	10	nil.

The symptoms resembled those described in the previous insect experiments. The single infection is attributed to chance because several gaps were subsequently found in the insect-proofing of the insectary.

Aphis maidis (Fitch).

The Maize aphid was tested as a vector by the methods described for the mealybug experiments. Although the insects appeared to feed on the test plants for at least twenty-four hours, no transmission of the lime die-back virus occurred. It is concluded that *Aphis maidis* is not a vector of the virus.

CONTROL OF THE DISEASE.

The disease is widespread over the Gold Coast Colony and Southern Ashanti, and is known to exist in British Mandated Togoland. It is impracticable to destroy and replace the infected plants because of the extensive area under cultivation, almost the whole of which is diseased but at the same time bearing a considerable yield. In addition, the presence of a very mobile vector would lead to a rapid re-infection of the replants. *Aphis citricidus* has been found on nearly all Citrus plants in the Gold Coast and on many indigenous *Rutaceae*.

Infected limes, budded on rough lemon about 10 to 15 years ago, retained their vigour, although they showed leaf symptoms and stem-pitting ; the lime industry is accordingly being rehabilitated by the replacement of moribund seedling limes with lime scions on rough lemon. They commence fruiting within three years of planting, and have grown vigorously for five years without signs of die-back. It is expected that they will yield an economic crop for at least ten years.

DISCUSSION.

A disease of the lime with vein-clearing symptoms similar to those described has been present in the West Indies for a long time. The disease has been ascribed to *Sphaerostilbe repens* B. et Br. but, as early as 1929, Ashby considered that this fungus was not a primary pathogen ; this view has been supported by Baker (1936) and Fennah (1942). Bain (1945), in a progress report, considered that shade, wind-protection and good husbandry seemed to retard and possibly prevent the occurrence of the disease.

In the Gold Coast, the trees in the plantation are closely planted and receive no cultivation by the peasant farmers. Whilst the lack of cultivation may have weakened the trees, the decline of the limes is caused by the virus; the gumming of the xylem and the abnormal starch translocation are sufficient to cause the death of the trees.

Costa *et al.* (1950) have suggested that tristeza and a stem-pitting of grapefruit, previously described by Oberhalzer *et al.* (1949), may be caused by the same virus or component of a virus complex. Costa used the lime as an indicator plant and describes similar symptoms to those observed on the Gold Coast ; moreover, *Aeglopsis Chevalièri* inoculated with tristeza displays the leaf distortion and vein-clearing described above. *Aphis citricidus* is a vector of tristeza (Menghini, 1946). McClean (1950), has shown that this aphid is a vector of the stem-pitting disease of grapefruit in South Africa. McClean used the lime as an indicator plant and again obtained similar symptoms to those described. Stem-pitting of grapefruit has been seen in the Gold Coast but has not been tested with the lime. Moreover, the sweet citrus (Table III) were shown to contain the lime die-back virus. Thus, it is assumed that the lime die-back disease of the Gold Coast is caused by a similar virus or virus complex to that described for tristeza and stem-pitting of grapefruit in South Africa and Brazil.

Like all Pseudococcids, *Ferrisia virgata* is rarely found on citrus in the Gold Coast, although it is a common pest of ornamental plants. It will, however, thrive if transferred to citrus but is not an important vector in the field.

SUMMARY.

A virus disease of limes in the Gold Coast is described. The disease causes gumming and hypertrophy of the xylem and impedes translocation of starch from the

PLATE I

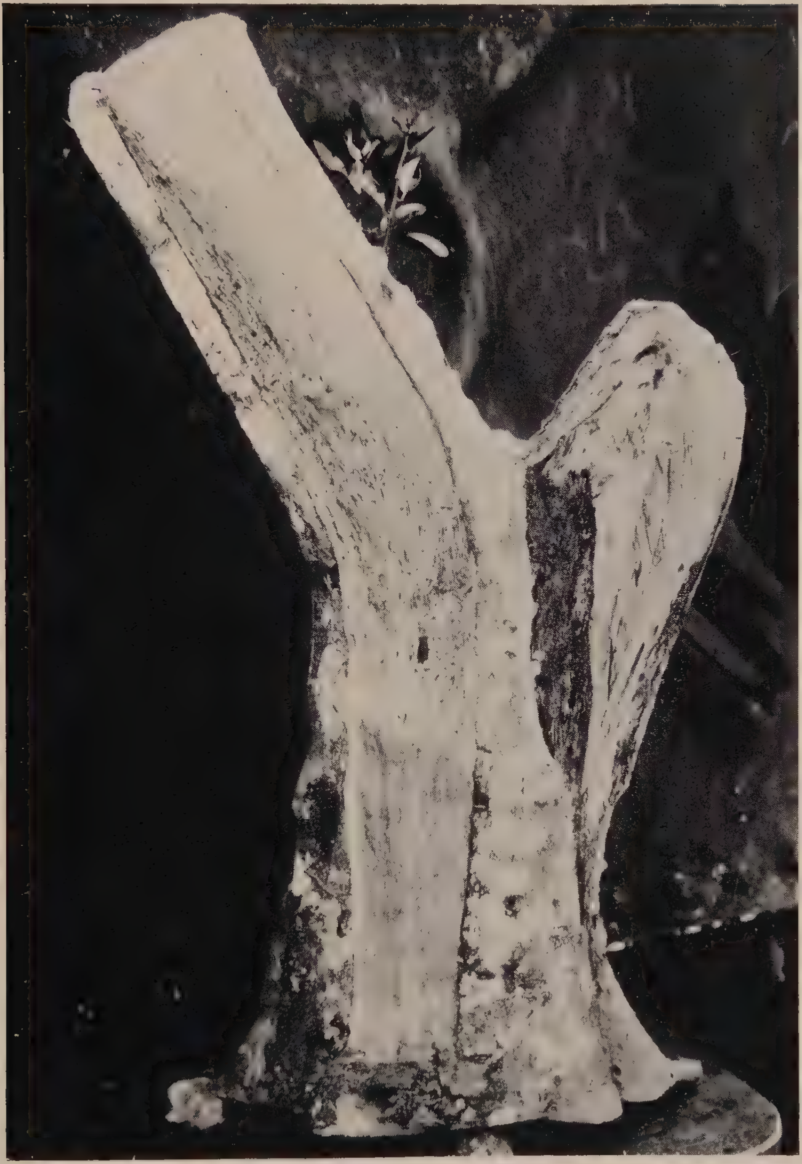

FIG. 1.

Lime budded on rough lemon. A strip of bark has been removed, revealing stem-pitting in the wood of the lime, but not in the tolerant rough lemon stock.

leaves. Attempts to transmit the virus by sap inoculation failed. Grafting experiments indicated that there are two viruses or strains, namely "die-back" and "little leaf". Rough lemon, sour orange, lake and Sampson tangelo when used as rootstocks, and three varieties of sweet orange, a tangerine and a grapefruit (all believed to be infected with tristeza), were found to be naturally infected with the lime virus. Rough lemon, lemon, Trinidad wild grapefruit, a Syrian bitter orange and *Clausena anisata* carried the lime virus without symptoms, while sour orange, citron, *Aeglopsis Chevalièri*, and *Afraegle paniculata* displayed symptoms. *Citropsis articulata* was killed by the virus.

Aphis citricidus (Kirk) transmitted the virus after one hour's feeding and the efficiency of transmission appeared to increase with length of feeding time, up to 24 hours. The mealybug, *Ferrisia virgata* (Cockerell), transmitted the virus after thirty hours' feeding time. Attempts to transmit the virus with *Aphis maidis* (Fitch) were unsuccessful.

The relationships of the disease are discussed and methods for control are described.

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GENETICAL STUDIES IN PEARS

VI. GIANT BUD SPORTS

By G. E. MARKS
John Innes Horticultural Institution, Bayfordbury, Hertford, Herts.

SYNOPSIS.

Two bud sports of pears, Improved Fertility and Double Williams', previously reported to be tetraploids, are now shown to be periclinal chimeras ; the epidermis is diploid and the inner tissues tetraploid.

Tetraploid somatic sports in apples, described in America by Einset, Blaser, and Imhoff (1947), and Derman and Darrow (1948), have been shown by these authors to be periclinal chimeras, the inner tissue being tetraploid with sixty-eight chromosomes and one or more outer layers being diploid with thirty-four chromosomes. In view of these findings with apples it was decided to re-examine certain giant-fruited sports in pears, namely two tetraploid sports, Improved Fertility and Double Williams', and a pear with large fruit alleged to be a sport from Winter Nelis.

Stomatal size and frequency were also studied in the first two and comparison was made with those features in the corresponding diploid varieties, but no suitable leaves were available for examination of the large-fruited Winter Nelis in this respect.

Materials and methods.

Developing flower and leaf buds, after being forced by bringing twigs into a warm greenhouse for a few days, were dissected and placed in Carnoy for two minutes ; they were fixed under reduced pressure for twenty-four hours in La Cour's 2BE, embedded in paraffin and sectioned at 14μ. Sections were stained by La Cour's crystal violet chromic acid method. Studies of the stomata were made on strips of lower epidermis fixed in acetic alcohol, stained and mounted in iodine-glycerine. Stomatal length was taken as a measure of size and the number of stomata per unit high power field as a measure of stomatal frequency. Those leaves were used which were judged by size, colour and texture to be mature.

Observations.

Improved Fertility.

The origin of the variety and its cytological behaviour have been described by Crane and Thomas (1939) who found the pollen mother cells to be tetraploid, reflecting the chromosome complement of the second histogen layer but not of the whole plant In the present study, sections of leaf bud show that while bundle sheath parenchyma (Plate II, Fig. 5) and cortical parenchyma are tetraploid, the epidermis is diploid. This variety is therefore a periclinal polyploid chimera.

Double Williams'.

Material of this variety was kindly supplied in 1939 by Dr. A. D. Shamel, Riverside, California. While all other tissues are tetraploid the epidermis is diploid (Plate I, Figs. 1 and 2). Therefore this variety is also a periclinal polyploid chimera.

Both Improved Fertility and Double Williams' are polyploid chimeras of Type I according to the classification of Einset, Blaser, and Imhoff (1947).

Large-fruited Winter Nelis.

Shamel (1937) describes the origin of this variety as a single tree with large fruits found in a plantation of Winter Nelis. Its pollen mother cells have thirty-four chromosomes and sections of somatic material show that all other tissues are also diploid. This giant-fruited form therefore is not polyploid in any tissue. Conceivably it may be a sport in respect of a genic mutation, but its original description as being a whole tree, rather than part of a tree bearing large fruits, suggests that it may be a new seedling and not a bud sport. That possibility is supported by an observation of Crane and Lewis (1940), mentioned below, and also by the fact that trees of large-fruited Winter Nelis at the John Innes Horticultural Institution grafted on quince rootstocks show a marked lack of vigour, apparently due to stock/scion incompatibility, a lack of vigour not shared by the normal Winter Nelis on the same rootstock.

STOMATAL SIZE AND FREQUENCY.

In both Improved Fertility and Double Williams' the epidermis is presumably genetically identical with that in the respective diploid counterpart. Stanton (unpublished work) finds no differences between Fertility and Improved Fertility in their reaction to clones of pear scab, *Venturia pirina* Aderh., a pathogen which primarily affects the epidermis. Crane and Lewis (1940), studying the epidermal foliar glands which occur on the petioles and mid-veins of pear leaves, found wide varietal differences but a close numerical correlation between the mean of both tetraploid sports and the diploid varieties from which they originated, though Winter Nelis and the large-fruited Winter Nelis differed widely in this respect.

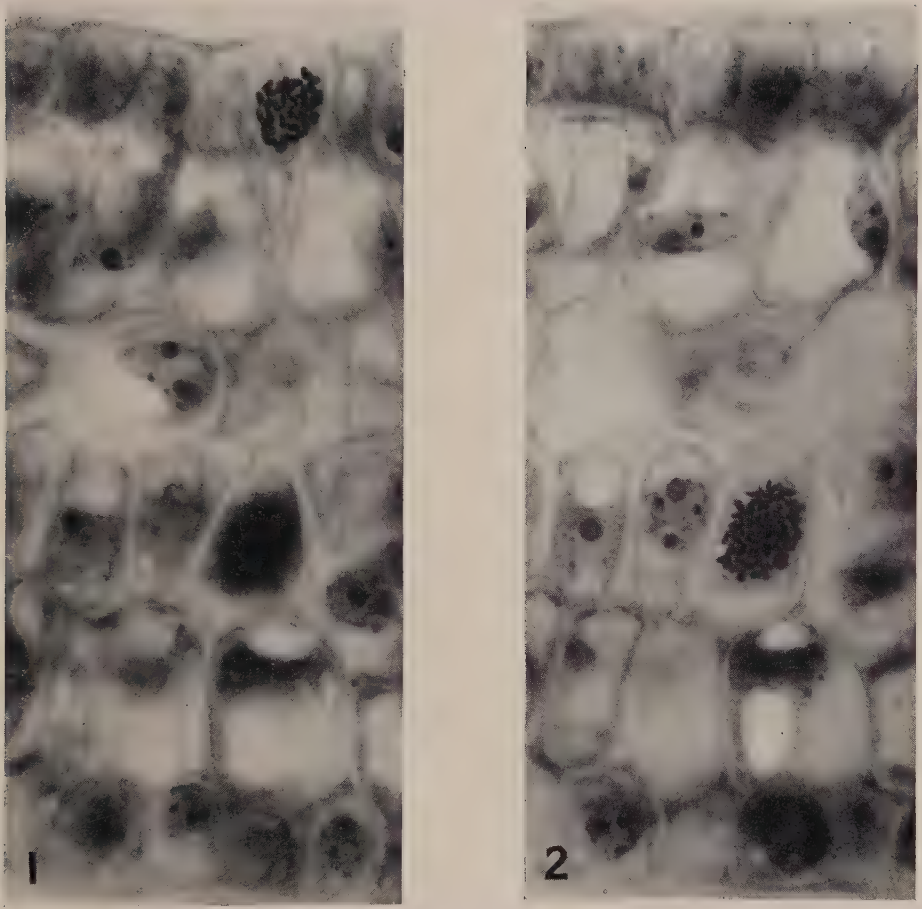
Differences may, however, be found between giant-fruited and diploid forms in epidermal characters and can be attributed to physiological influences set up by the different degrees of ploidy in the underlying tissues. Observations show (Table I and Fig. 1) that the stomata of Fertility and Improved Fertility are similar in size and in mean frequency but that in stomatal frequency from leaf to leaf there is a significantly greater range of variability in the diploid than in the tetraploid. Between

TABLE I.

Mean stomatal length and frequency.

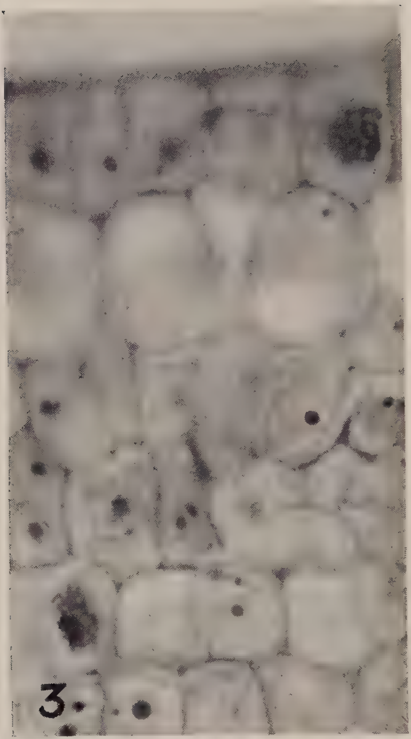
	Stomate length	Stomate frequency
	Mean of 200 readings	Mean of 300 readings
Fertility	21·60μ	12·22
Improved Fertility	21·80μ	12·83
Williams'	23·06μ	10·70
Double Williams'	22·90μ	9·57
SE_{MD}	±0·50	±0·57

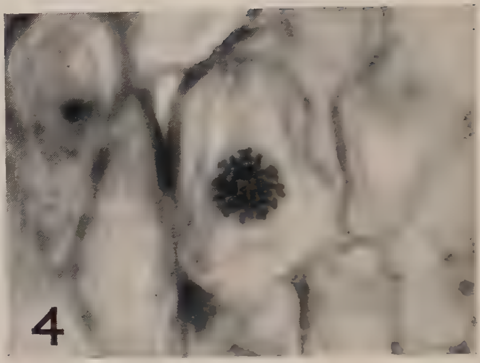
PLATE I.



FIGS. 1 and 2.
Double Williams'. T.S. young petal showing diploid epidermis and tetraploid internal tissue.

PLATE II.





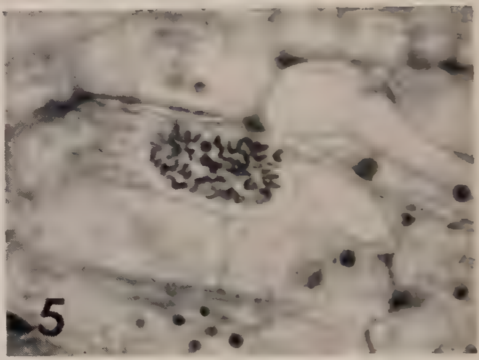


FIG. 3.
Fertility. T.S. stem near growing point showing diploid epidermis and diploid cortical parenchyma.

FIG. 4.
Fertility. Diploid cell in internal tissue of sepal.

FIG. 5.
Improved Fertility. Tetraploid cell in bundle sheath parenchyma of young leaf.
All photographs × 2,475.

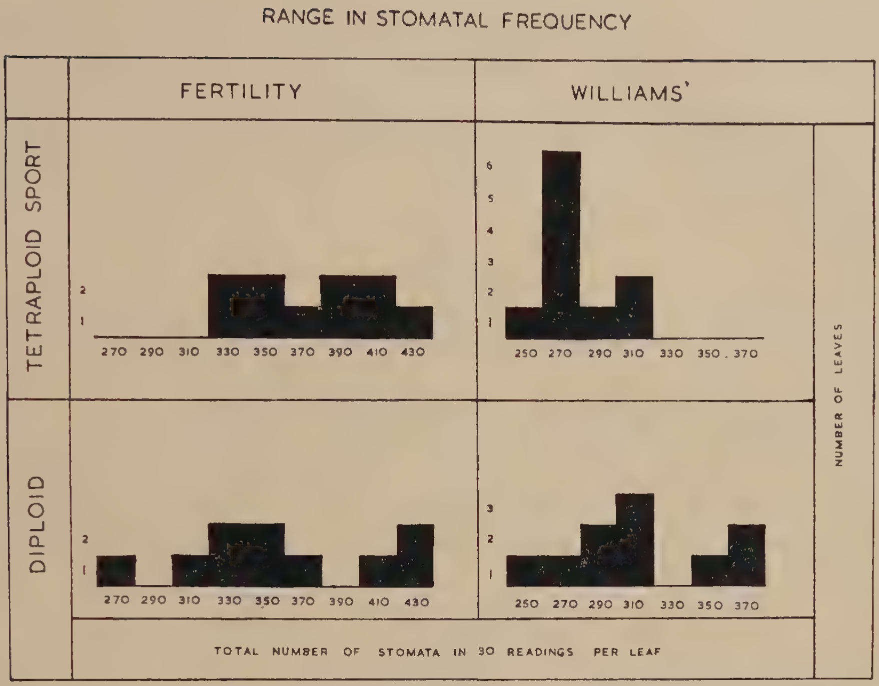


Fig. 1.

Williams' Bon Chrétien and Double Williams' there is again no difference in stomatal size, but there is a significantly lower frequency in Double Williams' as well as a lower range of variability in frequency from leaf to leaf. As there is a greater bulk of mesophyll tissue in the leaves of the giant forms, a " stretching " of the diploid epidermis may account for the lower frequency of stomata in Double Williams'. The greater stability in stomatal frequency observed in both the periclinal tetraploid sports may be due to their greater physiological stability. Fabergé (1936) found a parallel case in tomatoes where the fruit size within plants in the tetraploids was less variable than in the diploids.

Derman and Darrow (1948) show that the American periclinal tetraploid apple sports are slower-growing and produce comparatively smaller trees than the diploids. Similarly, Improved Fertility and Double Williams' are slower-growing than their respective diploids, though whether they will eventually make as large or larger trees remains to be seen. Probably the slower growth-rate of the periclinal polyploid sports may be due to a physiological limiting action of the diploid epidermis. The efficiency of the diploid epidermis can only be determined by comparing a complete tetraploid with a sport. This problem requires further study.

NATURE OF BUD SPORTS IN FRUIT TREES.

Bud sports may be classified in two types, those which originate and develop from normal buds, and those which arise adventitiously from endogenous buds. In the former, the change responsible for the sport must have been due to a mutation in the bud itself and, owing to the layered structure of the angiosperm growing point, identical gene mutations or changes in ploidy affecting all the initial cells must be exceedingly rare. Thus, bud sports developing from normal buds are usually chimeras. Sports arising from endogenous buds reflect the genetic composition of the inner tissues of the mother plant and are not likely to be chimeras ; they in fact illustrate the chimerical nature of the mother plant. Since endogenous buds are rare in fruit trees, it follows that all somatic sports which arise in them are probably periclinal chimeras.

SUMMARY.

The polyploid chimerical nature of two giant sports in pears, namely Improved Fertility and Double Williams', is described. Both are shown to have a diploid epidermis.

Tetraploid sports and diploid counterparts show no differences in stomatal size. The lower stomatal frequency in Double Williams' is attributed to a " stretching " of the epidermis due to the greater bulk of mesophyll in the leaf of the tetraploid. There is a greater uniformity in stomatal frequency from leaf to leaf within the tetraploids, a fact which indicates physiological stability greater than in the diploids.

It is suggested that all somatic sports in fruit are most probably periclinal chimeras.

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REVIEWS

THE CULTIVATION OF MUSHROOMS. By W. F. BEWLEY and J. HARNETT. (Anglo-Scottish Press. 1951. Third edition. Pp. 104, illus. Price 6s.)

Mushrooms have found increasing favour with the British public since the war, as is evidenced by the capacity of the markets to absorb the much greater production in the past few years.

The large increase in the number of growers has inevitably led to the demand for more literature on successful cultivation, because mushroom production is a continuous problem. Progressively rising costs compel growers to strive continually to secure more and more mushrooms from each ton of compost, and to this end I am confident they will welcome the new and revised edition of *The Cultivation of Mushrooms*. The pre-war editions were on the bookshelves of nearly every grower. The work is unique in that it was written by that well-known horticultural scientist, Dr. W. F. Bewley, in collaboration with a successful grower, the late Mr. J. Harnett. The book covers the field of production with commendable clarity, includes an excellent section on diseases and pests, their identification and control, and is well illustrated. I would like to see some reference to the "two zone", or more commonly termed "tray" system, also to peak heating with its impact on pH, moisture content of the compost, etc. However, no book on mushroom-growing tells the grower all he wants to know, because the answer to complex problems in this field are still being sought by research workers in this and other countries. The authors mention one of these problems when they state : "The temperature, humidity, and freshness of the air have an important effect on the crop, and a great deal of investigation is required concerning these conditions." What a flush of postulated theories is envisaged in that observation with the varying macro- and micro-climatic conditions in different types of growing houses, the variation in the ventilation of these, the multitude of different casing soils, all requiring their special handling technique ; here alone is the subject matter for a book.

The book is well worth its modest price, if it only helps the grower to appreciate the importance of trying to understand that one problem alone, or if he well digests the implications of the data given on experiments with various casing mediums.

The authors conclude by observing that the scientific principles which underlie mushroom-growing are not fully understood but, when the knowledge has been wrested from Nature, the maximum crops of today will no doubt become the average of tomorrow. That was first written seventeen years ago and, whilst some progress has been made in discovering Nature's secrets, it has been a slow process, and the happy state envisaged still seems a long way ahead. As a grower I find the subject a fascinating study which goes far to compensate for its difficulties. The book can help to minimize the difficulties.

A.G.P.

DICTIONARY OF GARDENING. Editor: F. J. CHITTENDEN. (Oxford : Clarendon Press. 1951. 4 vols. Pp. 2,316, illus. Price £10.)

The Council of the Royal Horticultural Society conferred a notable benefit on gardeners and botanists everywhere when they undertook to sponsor the revision of Nicholson's *Illustrated Dictionary of Gardening*. That trusty stand-by of Victorian horticulturists and, to a lessening extent, of their successors, can claim direct descent from Miller's *Gardener's Dictionary* of the 1720's and even a degree of kinship with John Parkinson's celebrated *Paradisus Terrestris* of 1629. The general scheme of Nicholson's Dictionary has not been changed, though many articles on subjects not touched on, and probably undreamt of by him, have been included. These special articles have been contributed by writers chosen for their pre-eminence in their subject. Many distinguished names adorn the list and it is a matter of very deep regret that a number of them, including the Editor, F. J. Chittenden, who was forced by the circumstances of the time to write a very large portion of the book himself, are now no longer with us.

Most of the Dictionary was prepared during the war years when the dispersal of British botanical libraries and herbaria rendered the investigation of problems of taxonomy and nomenclature difficult. Thus its sponsors lament that, in this respect, the book cannot be regarded as fully up-to-date. Except to the purist, who in any case will have other sources of information, this weakness will be insignificant and will be unnoticed by most of those whom the book is designed to help. Besides, with present day unflagging revision of plant nomenclature and the merciless scrapping of long-accepted names, a work of this sort becomes technically out-of-date from the moment of publication.

The arrangement is alphabetical. Descriptions are mainly confined to true botanical species (to which any popular English names are cross-referenced) and are restricted to salient features easily observed and to those characters which distinguish a species from its allies. To the description is added an occasional note of horticultural import, plants of special merit being starred. The general horticultural treatment of the genus as a whole under British conditions is described, often fully and always sufficiently. The number of names added since the last edition some 60 years ago is very great, particularly in regard to hardy plants from eastern Asia. The illustrations are all new and take the form of line drawings mostly from the living plant by leading botanical artists. They contribute materially to the value of the book by reason of the many uncommon plants depicted. A fifth volume is planned which, besides containing names of plants introduced since the preparation of the Dictionary, will contain lists of recommended varieties of such plants as are constantly being improved by hybridization and selection. This volume will be subject to periodical revision and reissue. That horticulture badly needed a modern work of this nature is evident. That the Royal Horticultural Society have provided it is to their lasting credit. That the venture will receive a grateful welcome from the gardening public is certain.

G.St.C.F.

THE ORIGIN, VARIATION, IMMUNITY AND BREEDING OF CULTIVATED PLANTS. Selected writings of N. I. VAVILOV, trans. by K. STARR CHESTER. (Waltham, Mass., Chronica Botanica Co., 1951, Chronica Botanica, Vol. 13, No. 1-6. Pp. viii+366, illus. Price $7.50.)

This volume provides for the first time an English translation of the more important writings of Vavilov and makes available much of the data assembled by him and his huge team of workers. The treatment of the subject is entirely objective and there is no trace of any " ideology ".

The second-half of the volume deals exclusively with wheat breeding and much of the first half refers to cereal and other agricultural crops. These sections are not of particular interest to the horticulturist but the remainder of the work will appeal to all who are interested in plant breeding.

Vavilov describes breeding as a science, an art and a branch of agricultural practice and considers that it covers a much wider field than does the science of genetics. He himself was interested in breeding in the wider sense and, in the introductory section, he mentions the various subjects to which the breeder must give his attention. These include the study of original material and of the origin of cultivated plants, variation, inter-relationships of environment and heredity, genetics, the theory underlying breeding practice and breeding with specific aims.

Phytogeography and the need for investigating the varietal plant resources of the world are given an important place. An extensive list of plants, grouped under their supposed centres of origin in the world, includes all the most important cultivated plants. The probable centres of origin have been established as the result of many expeditions undertaken by Russian plant investigators. The importance of climatic analogies in selecting species and varieties for introduction is mentioned, but a warning is also given that such analogies are not infallible and that direct tests are necessary in order to establish the suitability of plants to new conditions.

The " Law of Homologous Series ", formulated by Vavilov, is dealt with at length and supported by many particulars of heritable variable characters in various plants, especially in species of Gramineae and Papilionaceae. It is suggested that a study of this Law will indicate the possibility of the existence, or of the production by breeding, of forms of plants which are at present unknown.

A further section of the volume deals with the immunity of plants from the attacks of diseases and insect pests. The author discusses the nature of immunity, whether congenital or acquired, and the various types of resistance to attack, for instance those which can be classed as mechanical and those which are chemical in their action. Physiologic races of parasites receive attention and the influence of environment is considered, after which the genetics of immunity and the breeding of resistant varieties are discussed. Resistance to insect attack forms the subject of the concluding portion of this section.

This book deals only with investigations carried out before 1935 but it will be of permanent value and a lasting memorial to the work done by Vavilov in his regrettably short life. All plant breeders will welcome it for the mass of information and the extensive bibliographies it contains, and for the thought which it will stimulate.
G.T.S.

THE FRUIT GARDEN DISPLAYED. The Royal Horticultural Society. (Geoffrey Cumberlege, The Oxford University Press. 1951. Pp. 176, illus. Price 6s.)

This is a companion volume to *The Vegetable Garden Displayed* and the two certainly do make " Good Companions ". The object of the book is to provide a sort of running commentary for every practical operation of any importance that has to be carried out in the fruit garden. The commentary gives the reasons for doing things as well as the method of doing them. The book is garnished with 346 illustrations, including photographs, line drawings and diagrams, so that if any point in the commentary is missed by the reader, he can pick it up from one of these. What is more, the book can be taken out into the garden, propped up on the wall or fence, and worked from, just as may be done from *The Vegetable Garden Displayed*.

To begin with, there is a section on planning. This includes three scale-plans of gardens of different size, showing the actual layout of the various kinds of fruit and a really captivating photograph of one of the model fruit gardens at Wisley in blossom time. Next we have a section on preparing the site, and here we come upon portraits of our old friends from the companion volume who are digging, trenching and composting. Then comes a section on manuring in which Professor Wallace himself tells us in two pages all we need to know on the manuring of fruit trees and bushes.

Part I on soft fruits comes next, with sections on propagating, preparing site, planting, cultivating, training, picking, storing, diseases and pests, and lists of up-to-date varieties for each fruit in turn.

In Part II the tree fruits are described in much the same sequence, special attention being given to such vital operations as winter and summer pruning, budding, grafting, cross-pollination, choice of spraying tackle, and grass management. The illustrations are uniformly good.

Most of us have carried our copy of *The Vegetable Garden Displayed* in and out of the garden in all weathers for so long that it is almost fit for the compost heap by this time. I do not know how many amateur fruitgrowers there are in this country, but they will undoubtedly be pleased to hear that for the price of a taxi drive across London they can buy *The Fruit Garden Displayed* in a washable cover.

After reading the long list of distinguished contributors, it is only too clear that they must have chosen a really brilliant editor to produce such a well-balanced and sensible book. And having said that, let the last word be one of congratulation to Sir Ronald Hatton, the prime mover in the making of it, and who for over thirty years, at East Malling, has been preparing the way for so many of its recommendations.

N.B.B.

PUBLICATIONS RECEIVED.

THE FORTY-FOURTH ANNUAL REPORT OF THE GOVERNING BODY OF THE IMPERIAL COLLEGE OF SCIENCE AND TECHNOLOGY. 1951. Pp. 55.

CULINARY AND MEDICINAL HERBS. Bulletin No. 76 of the Ministry of Agriculture and Fisheries. (H.M.S.O. 1951. Price 1s. 9d. net.)

THE AMATEUR GARDENING DIARY AND HORTICULTURAL DIRECTORY 1953. Compiled by A. G. L. Hellyer. (London: W. H. & L. Collingridge, Ltd. 1952. Pp. 160. Price 8s. 3d.)

AMATEUR GARDENING ANNUAL. A PREVIEW OF THE YEAR'S WORK 1953. (London: W. H. & L. Collingridge, Ltd. 1952. Pp. 136, illus. Price 5s. 0d.)

LONG ASHTON RESEARCH STATION, 1903-1953

By Professor **B. T. P. BARKER, C.B.E.**

In 1893 Mr. Robert Neville Grenville, aided by the Bath and West and Southern Counties Society, started experiments on cider-making on the home farm of his estate at Butleigh Court, near Glastonbury. There, in a typical farm cider-house of the Somerset cider-orcharding area, was the real birthplace of the Long Ashton Research Station.

Ten years of experiments at Butleigh, directed by F. J. Lloyd, F.I.C., F.C.S., established the need for expanding the work, and a scheme for this purpose was prepared by the Board of Agriculture, with promise of financial support from the Bath and West Society and the counties of Devon, Gloucester, Hereford, Monmouth, Somerset and Worcester.

In 1903, a non-profitmaking, limited liability company of subscribing members and associates was founded under the name of the National Fruit and Cider Institute, and a 13½-acre site with a small unit of farm buildings, which were converted to comprise a laboratory, cider buildings and offices, was secured at Long Ashton. F. J. Lloyd was appointed as non-resident Director and B. T. P. Barker Assistant Director, becoming Director in 1905.

GROWTH

During the early years of the Institute's progress, the collaboration established with Professor J. H. Priestley of the then University College of Bristol paved the way for the association of the Institute with the University in 1912 as one of the Research Institutes set up by the Board of Agriculture and the Development Commission with grants made available under the Development Act of 1909. The Institute formed the nucleus of the University Department of Agriculture and Horticulture, and its administration was transferred to the Agricultural Committee of the University, on which were represented Council and Senate, the Board of Agriculture, the National Fruit and Cider Institute, and, later, representatives of the counties contributing to the University and of the fruit processing industries' associations. The National Fruit and Cider Institute, with its membership scheme, maintained its separate existence as an additional link with the horticultural and cider-making industries.

Under the new arrangement, the Long Ashton Institute received the official title of the Long Ashton Research Station and was given the responsibility of undertaking research on problems of fruit culture and on the practical control of pests and diseases of fruit trees, as well as on all aspects of cider-making and cider-orcharding. Concurrently the University was asked to administer one of the Provincial Advisory Centres then being established, and this service was added to the newly-formed Department of Agriculture and Horticulture. The latter arrangement continued until the inauguration of the National Agricultural Advisory Service in 1946.

In 1921, the Fruit and Vegetable Preservation Research Station at Chipping Campden, Gloucestershire, was included in the Department, of which it formed a part until 1952. In the meantime, the section of the Campden work dealing with domestic preservation of fruit and vegetables was transferred to the Long Ashton Station in 1930. Another addition was made in 1922 when a section for research and advisory work on basket willows was set up. During the 1939-45 war, a team of research workers was attached to the Station to investigate problems of mineral deficiencies in crop plants and, following a re-organization in 1952, this team became a special Agricultural Research Council Unit for the investigation of problems of plant nutrition, with particular reference to micronutrient elements. The unit continued to be housed at Long Ashton under the direction of Professor Wallace, who had become Director of the Research Station in 1943.

These successively widening interests necessitated frequent increases in staff, buildings and land. The scientific staff grew from 7 workers in 1919 to 22 in 1939 and 32 in 1952. Assistant scientific and office staff bring the present total up to 72.

In 1913 the original cider premises were greatly enlarged and a new laboratory was erected. This latter was extended in 1927, and in 1932, and a separate biology laboratory was built in 1947. A large pot-culture glasshouse was erected in 1928 with funds provided by the Empire Marketing Board, and a number of ancillary special-purpose buildings have since been added. Fenswood Farm, of 257 acres, on which the Research Station stands, was purchased by the University in 1920, and at present all suitable land is fully planted with experimental fruit plots. In collaboration with the contributing counties and the cider industry, the Station has also established many experimental cider orchards on farms.

RESEARCH WORK

The present research programme conserves the major aims defined when the Station was founded, namely that the staff should investigate the best methods of cultivation and utilization of all kinds of fruits and vegetables. The work is now divided into Sections, but there is a large measure of intersectional co-operation.

In pomology, major contributions are being made in studies of rootstock effect, tree form, and the action of growth-regulating substances on fruit plants. A list of approved cider varieties has been prepared by the Station Cider Advisory Committee, and the potentialities of bush trees for cider fruit production are being explored. The fruit-breeding work has already enriched the horticultural industry with two new dessert pears, two plums and three blackcurrant varieties of special merit.

The plant nutrition work at Long Ashton enjoys a world-wide reputation. The discovery in 1924 that the failure of fruit trees characterized by leaf scorch was caused by potash deficiency, revolutionized fruit production in England. Later, the roles of nitrogen, magnesium, iron, manganese, copper and zinc in fruit plants were elucidated, while field surveys established the critical soil factors for fruit-growing. Since 1939, farm and market-garden crops have been included in this work, and the visual symptoms of mineral deficiencies have been defined and published in a colour atlas. In recent years, fundamental studies on micro-nutrients and on the technique of experiments with pot-culture in sand have become outstanding features of the research programme.

An example of team work is provided by the investigations on pest and disease control, which have been undertaken jointly by chemists, entomologists and mycologists. An early service to the fruit-growing industry in 1921 was the introduction and improvement of the tar oil washes. Chemical and biological investigations have continued since that time to provide spraying programmes combining effectiveness, safety and economy. The special attention given to spraying machinery and methods of application has now made Long Ashton a centre for consultation on many diverse problems of pest and disease control arising throughout the Colonial Empire.

The influence of the work of the cider and fruit products section is apparent in the spectacular change in the status of cider-making over the past half-century. From being an unpredictable farm product of merely local interest, cider has become a widely-appreciated beverage of accepted standing and the basis of a flourishing industry. This progress is a reflection of the work of Long Ashton in developing a science of cider-making. The emphasis in this work has been on the fundamental importance of the quality of cider fruit and, on the manufacturing side, on the control of fermentation and the prevention of disorders. Studies on apple pomace, the primary by-product in cider manufacture, showed its value as a source of pectin, a material essential in jam-making. The jam manufacturers have also made wide use of the Station's introduction of the cold-process sulphur dioxide method for preserving fruit pulp.

In its work on other fruit products, Long Ashton originated the production in England of non-alcoholic apple juice and of blackcurrant syrup, which, since 1939, has been an important source of Vitamin C in the national diet.

In the section of domestic preservation of fruit and vegetables, the aim has been to establish the scientific principles underlying the methods of preservation. Precise standards for processing operations have been developed and the influences of methods and materials explored. Recently the work has been extended to cover preservation by freezing. Dissemination of the knowledge obtained, by means of courses and by bulletins, is an important feature of this section's activities.

OTHER DEVELOPMENTS

The Technical Section at the Research Station maintains liaison with other research and advisory centres and assists the large number of visitors (approximately 2,000 annually) who visit the Station from all parts of the world. The published work of the Station appears in its Annual Report, in the *Journal of Horticultural Science*, and in other appropriate scientific journals. The influence of the Station is further extended through those many ex-members of staff now holding important posts elsewhere in the field of agricultural and horticultural science.

The University of Bristol does not offer an undergraduate course in horticulture and the Research Station is not a teaching department in the usual sense of that term. Many distinguished overseas graduates have, however, worked at Long Ashton in the past, and it is a matter for regret that shortage of accommodation since the war has severely curtailed such international co-operation and is, in many other directions, hampering the activities of the Station. The implementing of the Station building scheme would ensure rapid developments in a research programme that is now firmly based on the substantial achievements of the past fifty years.

(*Received* 12/12/52.)

SPACING EXPERIMENTS ON VEGETABLES

VIII. THE RESPONSES OF SEVERAL VARIETIES OF GLOBE BEET, LONG BEET AND PARSNIPS TO CHANGES IN THE THINNING DISTANCE

By L. G. G. WARNE
Botany Department, Victoria University of Manchester

It is generally accepted that different varieties of root vegetables, although variable within themselves, do differ in their size and hence in their yielding capacity. Thus, Crimson King globe beet is described as larger than some other varieties (Anon. 1947), and Tender and True parsnip as being " moderate sized ", some other varieties presumably being larger. It is not known whether the different varieties differ in their space requirements and hence in the plant populations required to give maximum yields, or whether different varieties of the same root vegetable react similarly to alterations in the space available for their growth and development. To obtain information on these points, four varieties of long beet and three each of globe beet and parsnip have been grown at five thinning distances and the yields determined. The varieties were chosen to give a wide range of growth habits.

EXPERIMENTAL PROCEDURE.

The experiments were all carried out at the University of Manchester, Jodrell Bank Experimental Station, Lower Withington, Cheshire, on a heavy fertile loam which in the spring of 1950 received an application of 8 cwt. per acre of a mixture of three parts superphosphate of lime, two parts sulphate of ammonia, and one part sulphate of potash.

Globe beet. The three varieties, Crimson King, Red Globe (Detroit) and Turnip Rooted (Egyptian), were sown in rows 12 in. apart on 25th April, 1950, in plots randomized in five blocks. The main variety plots were split for thinning to the five nominal thinning distances of 1 in., 2 in., 4 in., 6 in. and 8 in. to give a total of 75 sub-plots. The procedure adopted for thinning was similar to that described previously (Warne, 1951). The plots were harvested late in August.

Long beet. Four varieties, Exhibition Black, Cheltenham Green Top, Covent Garden Red and Dobbie's Purple were sown in drills 16 in. apart on 5th May, 1950 in plots randomized in six blocks. The main variety plots were split for thinning to the five nominal thinning distances of 1 in., 2 in., 4 in., 6 in. and 8 in. to give a total of 120 sub-plots which were harvested in September.

Parsnips. Three varieties, Hollow Crown, Tender and True and Offenham were sown on 14th March, 1950 in drills 18 in. distant. The five nominal thinning distances employed were 2 in., 4 in., 6 in., 8 in. and 10 in. and the layout of the experiment was exactly as for the globe beet. The crop was harvested in October.

EXPERIMENTAL RESULTS.

These may be most conveniently presented under the two headings of 1, Yield and 2, Plant Competition, each crop being considered separately.

Yield.

Globe beet. The main results obtained are assembled in Table I. They are difficult to interpret because of the variations in plant population for the three varieties. Turnip Rooted with a mean yield of 453 cwt. per acre out-yielded the other two varieties. With Crimson King there is no significant difference over the

TABLE I.

Yield data for three varieties of globe beet (in 12 in. rows).

	Nominal thinning distance							
	1 in.	2 in.	4 in.	6 in.	8 in.	Mean	Signif. diff. (P=0·05) for comparing varieties	Mean for plots with maximum yields
" Theoretical " populations, thousands per acre	523	261	131	87	65			
	Populations in thousands per acre							
Crimson King . .	202	191	118	99	79	138		
Red Globe (Detroit) . .	179	161	109	91	70	122		
Turnip Rooted . .	335	229	138	116	93	182		
	Total yield of roots in cwt. per acre							
Crimson King . .	417	411	409	401	403	408		
Red Globe (Detroit) . .	442	432	402	392	377	409	32·4	
Turnip Rooted . .	461	501	467	423	413	453		
	Signif. diff. (P=0·05) for comparing treatment yields=53·5							
	Yields of " large " roots (over 1⅞ in. dia.) in cwt. per acre*							
Crimson King . .	383	390	404	396	397	394		
Red Globe (Detroit) . .	382	397	398	388	376	388	35·9	
Turnip Rooted . .	407	478	460	417	411	435		
	Signif. diff. (P=0·05) for comparing treatment yields=61							
	Yield of "saleable" roots (1⅞ in. to 3½ in.† dia.) in cwt. per acre.* (Treatments giving maximum yields in bold figures)							
Crimson King . .	**367**	**377**	**350**	271	158	305		365
Red Globe (Detroit) . .	**361**	**394**	**347**	255	146	301	34·8	367
Turnip Rooted . .	**378**	**391**	227	124	61	236		384
	Signif. diff. (P=0·05) for comparing treatment yields=63							

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* A minimum diameter for " large " roots adopted before the publication, by the Ministry of Agriculture, of Marketing Leaflet No. 102, 1948.

† Maximum diameter suggested by the Ministry of Agriculture, 1948.

whole population range tested, but the yields of the other varieties are significantly reduced at the smaller plant populations. Yields of "large" roots do not differ significantly over the population range tested, except for the Turnip Rooted variety, for which they are significantly higher at 138,000 and 229,000 plants to the acre than at higher or lower population densities. Practically, however, interest centres on the yield of saleable roots, i.e. those of diameters 1⅞ in. to 3½ in., and with the two round types maximum yields are given with populations of not less than 118,000 per acre for Crimson King and 109,000 per acre for Red Globe (Detroit), figures agreeing almost exactly with those suggested earlier (Warne, 1952) as the minimum population desirable for the variety Crimson King. For the Turnip Rooted variety a higher population, namely 229,000, appears necessary. This is undoubtedly the result of morphological rather than of physiological differences between the varieties. Thus, for the two round varieties, roots of 1⅞ in. and 3½ in. diameter weigh 2·44 oz. and 13·1 oz. respectively. For the Turnip Rooted variety, the corresponding weights are 2·16 and 9·9 oz. These differences have little effect at the lower limit of 1⅞ in. but a large effect at the upper limit (3½ in.), so that, whilst for the Turnip Rooted variety at the 4 in. thinning distance 28% of the roots (i.e. approximately half the total weight) are rejected as being too large, the other two varieties average 8% rejected or 13% of the total weight. The difference is equally striking within the population range 91,000-99,000 per acre. For the three varieties (in the order of the Table) 17%, 20% and 51% of the roots are rejected as being too large, i.e. 31%, 34% and 85% of the total weight. It is clear, therefore, that a closer stand of the Turnip Rooted than of the round varieties is necessary to avoid the production of roots of excessive diameter. Further, whilst the Turnip Rooted variety is higher yielding than the other two varieties for comparable populations, the elimination of too large and too small roots reduces the maximum yields of saleable roots to a point where they do not differ significantly, i.e. 365, 367 and 384 cwt. respectively. These maxima, however, were obtained with such differing populations as to suggest that, for any comparison of yields of the three varieties, experiments carried out at several spacings would be necessary.

Long beet. Table II contains the yield data for the long beet. As with the globe beet, population differences between varieties render interpretation of the yield data difficult, but with no variety does the total yield of roots depend on the population within the approximate range of 50,000 to 100,000 plants per acre. Within this range, yields of "large" roots remain unchanged for the varieties Exhibition Black and Cheltenham Green Top, while the other two varieties do not alter appreciably unless this population is greatly exceeded. In a previous experiment (Warne, 1951) a population of 184,000 per acre of the variety Exhibition Black did not prove deleterious, but in the present experiment 168,700 plants per acre of the Covent Garden Red variety gave a reduced yield of "large" roots. In spite of the difficulty of attaining great precision in experiments where population differences between varieties occur, where the population can be only approximately controlled and where the "saleable" yield is an arbitrarily chosen fraction of the total crop, the data presented here do not contradict the previous conclusion (Warne, 1952), i.e. that maximum yields of long beet are assured with populations within the range 70,000 to 135,000 per acre with a possible extension of these limits. The data from this experiment do not suggest that different populations are necessary to give maximum yields of large roots, although the mean maxima differ for the four varieties, i.e. 381, 347, 306 and 332 cwt. per acre (see Table II) and the varieties are known to differ in other respects (Warne, 1950).

TABLE II.

Yield data for four varieties of long beet (in 16 in. rows).

	Nominal thinning distance							
	1 in.	2 in.	4 in.	6 in.	8 in.	Mean	Signif. diff. (P=0·05) for comparing varieties	Mean for plots with maximum yields
" Theoretical " populations, thousands per acre	391	195	98	65	49			
	Populations in thousands per acre							
Exhibition Black ..	101·5	96·5	69·0	60·4	47·7	75·0		
Cheltenham Green Top	104·4	86·0	68·5	54·4	49·5	72·6		
Covent Garden Red ..	216·5	168·7	94·9	69·4	55·2	120·9		
Dobbie's Purple ..	164·3	131·3	84·4	65·3	50·8	99·2		
	Yields of roots : cwt. per acre							
Exhibition Black ..	393	415	398	401	381	398		
Cheltenham Green Top	370	355	363	356	369	363		
Covent Garden Red ..	377	388	346	344	331	357	44	
Dobbie's Purple ..	390	407	377	363	352	378		
	Signif. diff. (P=0·05) for comparing treatment yields=49							
	Yield of " large " roots (over 1⅝ in. dia.) cwt. per acre. (Treatments giving maximum yields in bold figures)							
Exhibition Black ..	**357**	**388**	**386**	**395**	**380**	381		381
Cheltenham Green Top	**333**	**335**	**351**	**352**	**363**	347	46	347
Covent Garden Red ..	221	265	**293**	**305**	**320**	281		306
Dobbie's Purple ..	270	**318**	**332**	**337**	**342**	320		332
	Signif. diff. (P=0·05) for comparing treatment yields=47							

Parsnips. The yields of the three varieties of parsnips are given in Table III. Because of the great discrepancy between the varietal populations at the 2 in. thinning distance, discussion must be confined to the data for the 4 in., 6 in., 8 in. and 10 in. plots. The total yield of roots falls significantly when the thinning distance is over 8 in. for the varieties Hollow Crown and Offenham, but does not change between 4 in. and 10 in. for Tender and True, whilst with no variety does the yield of large roots change significantly over the population range of approximately 35,000 to 80,000 plants per acre and there is, therefore, no evidence that the different varieties demand different population densities for maximum yields, although, as with the

TABLE III.

Yield data for three varieties of parsnips (in 18 in. rows).

	Nominal thinning distance							
	2 in.	4 in.	6 in.	8 in.	10 in.	Mean	Mean (omitting 2 in. plots)	Signif. diff. (P=0·05) for varieties
" Theoretical " populations, thousands per acre ..	174·2	87·1	58·1	43·6	34·8			
Variety	*Populations in thousands per acre*							
Hollow Crown	154·0	81·1	58·9	43·4	38·4	75·2	55·4	
Tender and True	156·0	81·9	58·6	43·1	38·9	75·7	55·6	
Offenham	115·5	84·2	59·0	45·0	34·8	67·7	55·7	
	Yields of roots : in cwt. per acre							
Hollow Crown	336	346	328	304	281	319	315	
Tender and True	329	355	357	351	347	348	352	46·2
Offenham	319	361	330	350	304	333	336	
Mean	328	354	338	335	311			
	Signif. diffs. (P=0·05) for comparing treatment yields =43, and for comparing thinning means=25							
	Yield of " large " roots (over 2 in. diam.): cwt. per acre*							
Hollow Crown	121	279	306	298	273	255	289	
Tender and True	95	307	353	337	330	284	332	22·0†
Offenham	143	322	311	345	299	284	319	
Mean	120	303	323	327	301			
	Signif. diffs. (P=0·05) for comparing treatment yields =52† and for comparing thinning means=34†							

* A minimum diameter adopted before the publication, by the Ministry of Agriculture, of Marketing Leaflet No. 102, 1948.

† Results for 2 in. plots omitted.

long beet, the yields do differ. The populations of the three varieties are so nearly alike (except at 2 in.) that the mean yields for each thinning distance are of interest. It is seen in Table III that the mean total yield and that of large roots fall significantly when the 8 in. thinning distance is exceeded. Hence maximum yields of large roots are given with populations between 43,800 and 82,400 per acre, although with no single variety was it possible to show that a further reduction in the plant population to approximately 37,000 adversely affects the yield of large roots. Mean yields of large roots are, for the three varieties, 289, 332 and 319 cwt. per acre respectively (significant difference, $P=0{\cdot}05,=22{\cdot}0$).

Although the varietal differences are small, the fact that only with some varieties does the total yield change within the population range, indicates that they do react differently to changes in the spacing. The yields of large roots, however, suggest that these small differences are of little or no practical importance, despite the fact that both physiological and morphological characters affect the yields. For the three varieties, roots of 2 in. diameter (the grading limit) weigh 5·5, 6·6 and 5·2 oz. respectively, but this has not greatly affected the proportion of the crop graded out as " small ". In previous experiments (Warne, 1952) the yield of " large " roots fell for populations below 59,000 plants per acre and, although in this experiment maximum yields were given with fewer plants, the data presented here do not contradict the earlier conclusion that populations of from 59,000 to 86,000 can be *depended* upon to give maximum yields.

It is concluded from these experiments that, in practice, physiological differences between the varieties of root vegetables tested are not large enough to affect the populations required for maximum yields of saleable roots, but that sometimes morphological features of the varieties, by affecting the ratio of root diameter/weight, alter the proportion of the crop which falls within an acceptable diameter range and so may affect the level of population necessary to produce maximum yields.

Plant competition.

That total yields often changed only slightly over the range of population densities common to the several varieties tested suggests that the plants of the

TABLE IV.

Regressions of available area (A), *in sq. in., on mean root weight* (W), *in oz., for globe beet, long beet and parsnips.*

$(W=x(A)^{y})$.

Globe beet		Long beet		Parsnips	
Variety		Variety		Variety	
Crimson King	$0{\cdot}13(A)^{0{\cdot}97}$	Exhibition Black	$0{\cdot}14(A)^{0{\cdot}86}$	Hollow Crown	$0{\cdot}27(A)^{0{\cdot}72}$
Red Globe (Detroit)	$0{\cdot}12(A)^{0{\cdot}93}$	Cheltenham Green Top	$0{\cdot}11(A)^{0{\cdot}97}$	Tender and True	$0{\cdot}22(A)^{0{\cdot}84}$
Turnip Rooted	$0{\cdot}34(A)^{0{\cdot}74}$	Covent Garden Red	$0{\cdot}12(A)^{0{\cdot}92}$	Offenham	$0{\cdot}22(A)^{0{\cdot}82}$
		Dobbie's Purple	$0{\cdot}16(A)^{0{\cdot}80}$		

different varieties responded to a similar, although not identical, extent to changes in the space available for their growth. As in previous work, regressions of available area on root weight have been calculated but, as any regression so calculated can only apply to the range of " available areas " tested, the calculations have been based only on the values for those sub-plots in which populations fell within the range common to all the varieties. For globe beet this included all plots the range population of which was equivalent to less than 224,000 ; for long beet, less than 124,000 ; and for parsnips less than 92,000 per acre. The results obtained are tabulated in Table IV.

DISCUSSION.

The values given above are only a reflection of the differences in total yield noted earlier and they should be interpreted with much caution. Thus, with parsnips, root weight is less dependent on available area with Hollow Crown than with Tender and True and Offenham; this does not indicate that Hollow Crown is more resistant to the effects of close spacing but that it is unable to use efficiently a large area when this is available. Thus this variety has a significantly lower total yield (but not yield of large roots) than the other varieties when widely spaced (8 in.), but not when closely spaced (4 in.).

The data presented indicate how beet varieties differ in yielding capacity and in the morphology of their storage organs, and it is clear that they also respond differentially to alterations in the space available for their growth. Thus Turnip Rooted " globe " beet is much less responsive to increases in the available space than are the two round varieties ; similarly, Dobbie's Purple long beet responds less than the other long beets. Thus, when the area per plant is increased from 36 to 72 sq. in., the Turnip Rooted variety of beet responds with a 68% increase in weight as against 95% with the other two varieties. Similarly, doubling the available area per plant from 48 to 96 sq. in. for long beet results in an increase in root weight of only 73% for Dobbie's Purple as against 96% for Cheltenham Green Top. Varietal differences in the water relations and in the development of lateral roots for long beet have been pointed out elsewhere (Warne, 1950) ; others came to light during this investigation. The four long beets (in the order of Table II) had root/top ratios of 4·27, 4·58, 2·38 and 1·90. In this respect the varieties fall into two groups which, as has been pointed out elsewhere, differ also in other characters (Warne, 1950). Differences in their lateral root development were reflected in the amounts of soil adhering to the roots at harvest and, for roots lifted under wet conditions, the " dirt tare " (i.e. weight of soil adhering to 100 lb. of roots after normal cleaning) varied from 2·7 lb. for Exhibition Black to 9·7 lb. for Covent Garden Red. Smaller varietal effects occurred with globe beet, where the root/top ratios for the three varieties (in the order of Table II) were 3·34, 3·24 and 2·72.

It is clear that the several varieties of the three types of root vegetables tested differ both morphologically and physiologically ; and this affects their response to changes in the space available for their growth. Equally, these physiological differences are not large enough materially to affect the populations needed to give maximum yields of saleable roots. In this respect morphological features tend to outweigh in importance physiological ones. Thus the data emphasize the difficulties of trials of this kind. However, provided only varieties of similar morphology are compared, populations within the limits required to give maximum yields should give a valid comparison of varieties. When important morphological differences exist, estimates of total yield may be more reliable than those restricted to roots of a certain size as a criterion of cropping ability, leaving the question of diameter adjustment by spacing alterations for separate consideration.

SUMMARY.

1. Three varieties of parsnip and globe beet and four of long beet were grown at five thinning distances.

2. The varieties differed in their yielding capacity and in their response (as measured by root weight) to changes in the space available for their growth.

3. The physiological differences were not large enough substantially to affect the population range within which maximum yields of saleable roots were produced.

4. In determining desirable populations for different varieties of these crops, morphological characters of the varieties have more effect than the physiological differences between them.

5. Special varietal features observed in the course of the experiment included :

(*a*) The relative inability of Hollow Crown parsnip and of Dobbie's Purple long beet to use efficiently the available space at wide thinning distances.

(*b*) The relative ability of Turnip Rooted beet to grow satisfactorily at close spacings.

(*c*) The exceptionally clean roots of Exhibition Black long beet.

(*d*) The differences in leaf/top ratio, the four long beet varieties falling into two distinct groups.

ACKNOWLEDGMENTS.

Acknowledgments are due to Mr. G. E. Davies, who was responsible for the collection of yield data, to Mr. F. H. Wallen, who efficiently supervised the cultural operations, and to the Agricultural Research Council for a grant which made this work possible.

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A FROST ALARM WITH ADJUSTABLE TEMPERATURE SETTING

By **H. R. HART**

Dominion Physical Laboratory, New Zealand Department of Scientific and Industrial Research.

A NEW type of frost alarm has been made to a specification formulated after discussions with interested persons and organizations concerned with pomology.

SPECIFICATION.

1. *Range.*

The alarm must be adjustable so that it can be pre-set to any temperature in the range 20° F. to 40° F.

2. *Repeatability.*

The alarm must repeat to within ± 1° F. of the nominal pre-set temperature.

3. *Operation.*

The alarm and warning device must operate at a distance from the temperature-sensitive element.

4. *Total error and lag.*

The total error of the instrument over the working range, including lag in temperature response behind the accepted meteorological frost-registering element

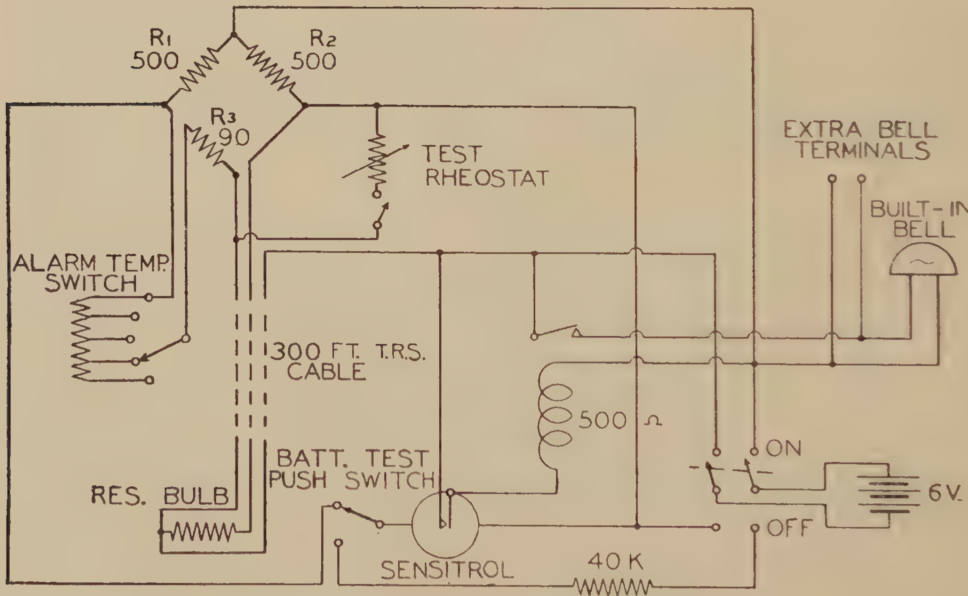
R1
500
R2
500
R3
90
TEST
RHEOSTAT
EXTRA BELL
TERMINALS
BUILT-IN
BELL
ALARM TEMP.
SWITCH
300 FT. T.R.S.
CABLE
500 Ω
ON
6V.
BATT. TEST
PUSH SWITCH
RES. BULB
OFF
SENSITROL
40 K

FIG. 1.
Circuit Diagram.

(alcohol-in-glass thermometer), must not be greater than 1° F. when the temperature falls at a rate of 1° F. in 10 minutes, under all conditions, i.e. with or without air movement. The total error must not exceed 1° F. throughout the life of the instrument.

5. *Construction.*

The exposed portion of the alarm, including the temperature-sensitive element, must not be affected by moisture, dust, etc.

6. *Power supply.*

A battery-operated instrument is preferred to one using mains supply. In the latter, the circuit must be arranged to give warning in the event of a power failure.

Further, it is desirable, though not altogether necessary, that a continuous indication of temperature should be provided, that the alarm should be easily regulated and used by non-technical people and that a test switch should be provided to enable the warning device to be tested, regardless of the temperature at the time.

This specification precludes the use of certain types of thermostats and other appliances which might be thought suitable for use as frost alarms.

DESCRIPTION.

The instrument embodies a Wheatstone bridge (Fig. 1) of which one arm is a temperature-sensitive resistance bulb (Fig. 2), two other arms are fixed resistors and the remaining arm is a fixed resistor in series with a tapped resistor adjustable by a selector switch having a scale from 20° F. to 40° F. When the resistance bulb reaches the temperature to which the selector switch is set, the bridge becomes balanced and the alarm rings. Under both laboratory and field conditions the alarm operated consistently to within ± 0·5° F. of the pre-set temperature. Its lag is considerably less than that of a standard meteorological-type minimum thermometer. This rapidity of response is largely due to the construction of the resistance bulb, which has a fine nickel wire, wound on a former, in good thermal contact with its sheath. The sheath is also fitted with a number of blackened copper fins. The resistance bulb is mounted under a screen (Fig. 3) to prevent radiation skywards and is connected to the cabinet (Fig. 4) by 3-core cable. The cabinet is intended to be installed indoors, together with a 6-volt battery. The temperature-selector switch can be made to operate over any desired range of temperatures : in this case a 21-position switch has been used to make the alarm operate in 1° F. steps between 20° F. and 40° F. (For simplicity, only five positions are shown in Fig. 1.) The instrument relay is a Weston " Sensitrol ", which was originally calibrated from 0 to 2·5 microamp. The dial was re-graduated 0° F. to 10° F. in order to make the relay indicate the difference between the selector-switch setting and the temperature of the resistance bulb. The temperature of the resistance bulb is the selector-switch setting plus the relay indication. Provision is made for checking the battery voltage to ensure that it does not fall below 5·5 volts. Changes in battery voltage do not affect the operating point of the alarm, since it operates only when the bridge is balanced. A test rheostat enables the instrument to be checked at any time, regardless of the temperature of the resistance bulb.

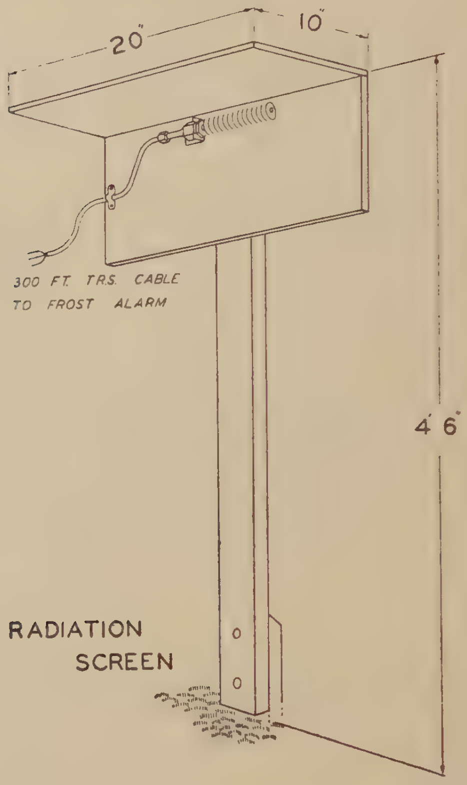
20"
10"
4' 6"
300 FT. T.R.S. CABLE
TO FROST ALARM
RADIATION
SCREEN

FIG. 3.
Resistance bulb mounted under screen.

ACKNOWLEDGMENT.

The work described in this paper was carried out in the Dominion Physical Laboratory of the New Zealand Department of Scientific and Industrial Research, and is published with the permission of the Secretary of the Department.

(*Received* 16/8/51.)

A FROST ALARM WITH ADJUSTABLE TEMPERATURE SETTING. BY H. R. HART.

PLATE I.

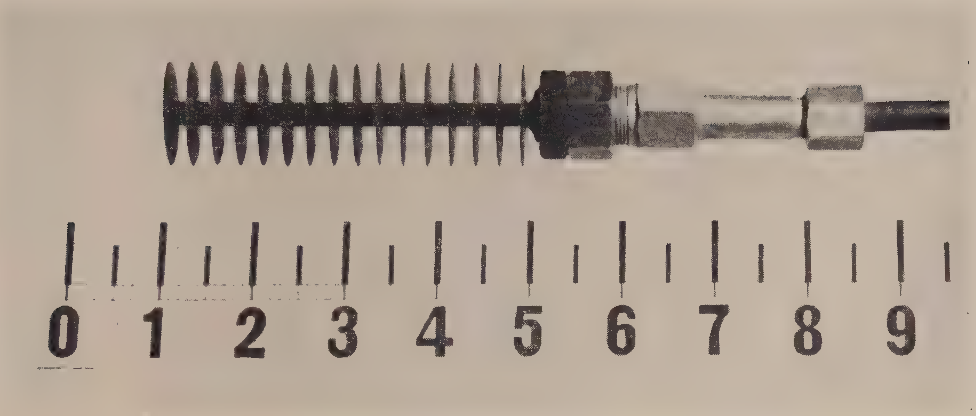
0 1 2 3 4 5 6 7 8 9

FIG. 2.
Resistance bulb.

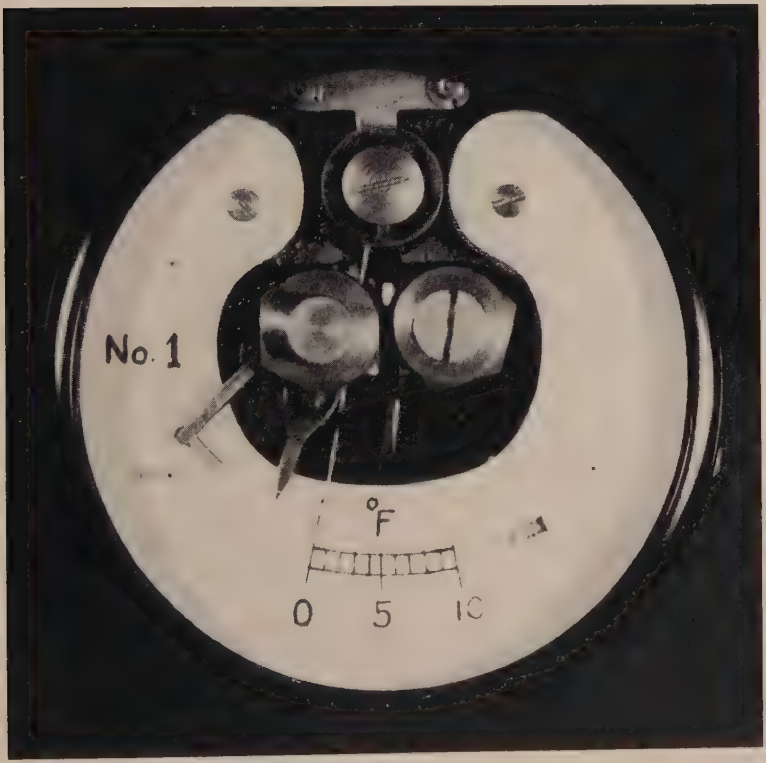

FIG. 5.
Indicator dial.

[*face page 162*

PLATE II.

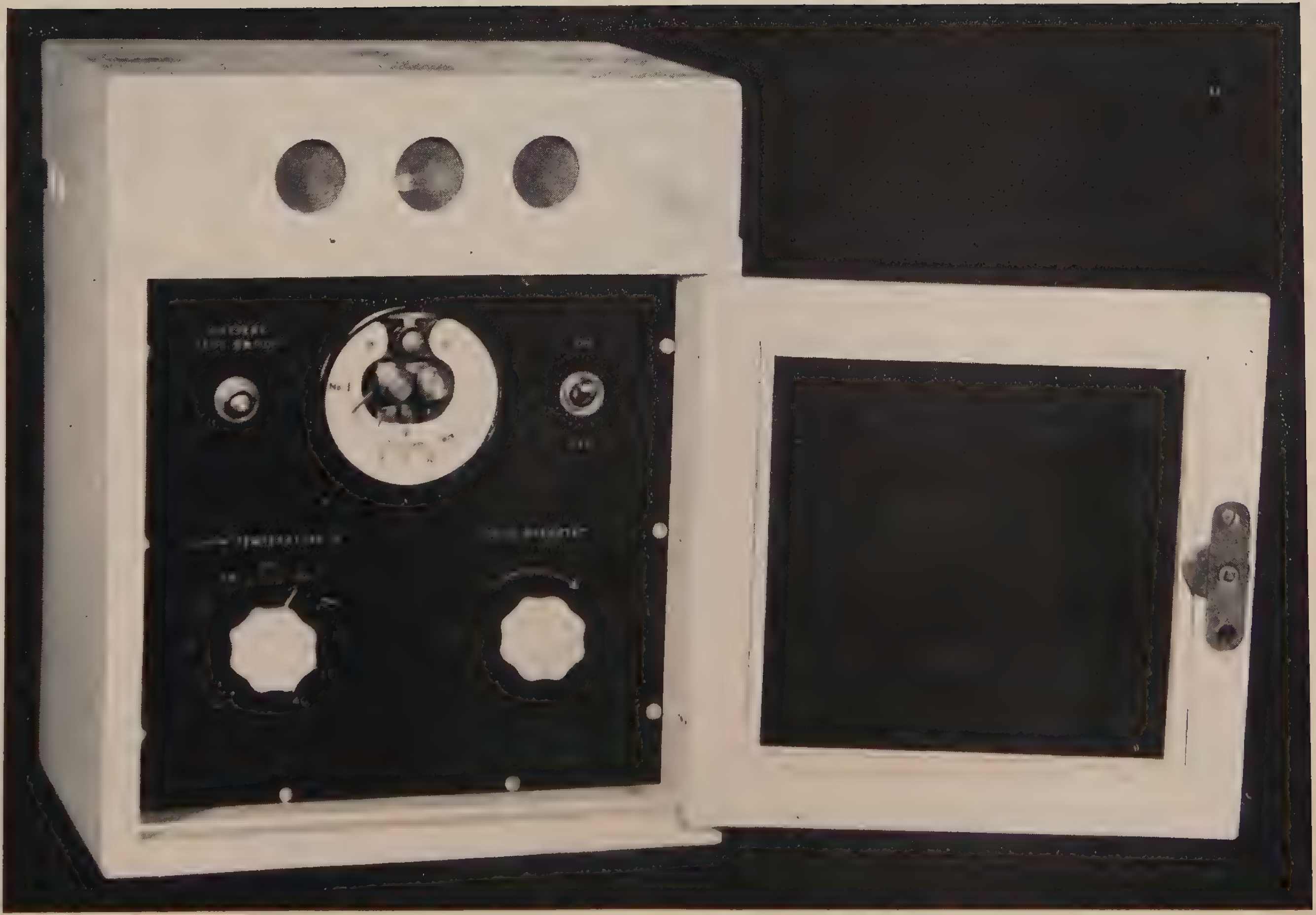

FIG. 4.
Cabinet.

THE USE OF SOME NEWER INSECTICIDES FOR THE CONTROL OF APPLE SAWFLY, *HOPLOCAMPA TESTUDINEA* (KLUG)

By A. H. M. KIRBY and R. G. GAMBRILL
East Malling Research Station, Kent

ALTHOUGH an infestation by Apple Sawfly was reported over a century ago (Westwood, 1847), no means of chemical control of this pest was suggested until Grubb and Bagenal (1924) reported good results with post-blossom lead arsenate-lime sulphur applications. Petherbridge and Tunnington (1929) reported failure with lead arsenate but success with nicotine at 0·0625%, plus 1% soft soap as spreader, immediately after petal-fall. These workers found two applications more effective than one, but the fruit size was reduced. The superiority of nicotine over lead arsenate was confirmed by Kearns and Swarbrick (1933) and Hey and Steer (1934). Derris was tried by Austin, Jary and Martin (1932) but was found inferior to nicotine by Hey and Steer (1934) and Kearns, Marsh and Martin (1936, 1937), although it was recommended for control of migrating larvae by Steer and Thomas (1935).

The use of nicotine before complete petal-fall, at 0·05%, with a suitable wetting-agent and sufficient pressure to ensure entry of the spray into the calyx-cup of the fruitlets, became the standard method for control of Apple Sawfly. But it has been common experience that the procedure is unreliable. Some factors governing success in the use of this insecticide for the purpose are considered in the subsequent paper (page 170) (Kirby and McKinlay, 1953), but the need for a more persistent insecticide has been felt for some time. The chlorinated hydrocarbons and some of the organophosphorus compounds come into this category, and results of field trials with several such insecticides have been reported by Davies and Eaton (1950), who found that the use of the potent but non-persistent insecticide, HETP, either at 80% petal-fall or at peak egg-hatch, was valueless but that persistent insecticides such as chlordane, γ-benzene hexachloride and parathion controlled this pest, even in a year when nicotine was only partially effective. The present authors have continued these trials, and this paper reports work carried out with parathion in 1949 and with several insecticides in 1950.

TRIAL WITH PARATHION (1949).

As few sawflies were visiting the trees used by Davies and Eaton (1950) in the earlier trials, this trial was carried out on mature trees of Worcester Pearmain and Cox's Orange Pippin on Ditton Court Farm, adjacent to the Station.

Materials.

One promising insecticide, parathion, was used at three dilutions. The 75% pure sample was formulated as follows: 12·5 parts di-octyl sodium sulphosuccinate (Aerosol OT) and 20 parts *cyclo*hexylamine dodecyl sulphate (MB320) were dissolved in 200 parts diacetone alcohol, and the calculated quantity of parathion added; on pouring into sufficient water, an emulsion was formed containing 0·2% diacetone alcohol, 0·02% MB320 and 0·0125% Aerosol OT.

Treatments.

The treatments applied, with timing, are summarised in Table I.

TABLE I.

Treatments on Cox's Orange Pippin and Worcester Pearmain 1949.

Treatment	Concentration	Timing	Replicates
A. Parathion	0·02%	Petal-fall	4
B. Parathion	0·005%	Petal-fall	4
C. Parathion	0·00125%	Petal-fall	4
D. Control	—	—	1
E. Parathion	0·00125%	Egg-hatch	1

The control trees, treatment D, received 1% lime-sulphur only ; this fungicide was added at the same concentration to all parathion sprays.

Treatments A, B and C were randomized in four replicate blocks ; Worcester trees were in a single row and three trees were used for each treatment, the leeward tree of each plot being recorded. Cox trees were also in a row but this included one pear tree in each four trees ; recording was on the most southerly Cox tree in every plot.

Spraying data.

Petal-fall was well advanced by 10th May, approaching 80%. Sprays were applied on this date by a commercial machine, employing twin-nozzle lances, with a pressure of at least 200 lb. per sq. in. A northerly breeze caused moderate drifting along the rows, but nearly all the recorded trees had two guard-trees to protect them.

No hatching was observed until 17th May, but peak hatch was reached on the 19th and 20th, and hatching was almost complete by the 23rd. Considerable burrowing had occurred on nicotine-sprayed trees in the same orchard by the 20th. It was decided to try the lowest concentration of parathion as an egg-hatch spray ; treatment E was therefore applied to previously unsprayed trees on the 19th.

The weather on 10th May was sunny and mild. Meteorological observations in a neighbouring orchard showed a maximum temperature of 56° F. and a minimum of 29° F. ; there was only a trace rainfall on the night of the 10th and no rain until the 14th. The 19th was sunny and warm ; maximum temperature was 66° F., and minimum 37° F. ; no rain fell.

Degree of control.

Dropped fruitlets were gathered at frequent intervals and the percentage infested recorded ; the infestation of the picked crop was also assessed. As the controls, D, and the egg-hatch parathion treatment, E, were not randomized among the other treatments, no statistical analysis of these results was possible, but an analysis of the results from treatments A to C has been made and the figures, together with the infestation data for all treatments, are recorded in Table II.

It will be seen that increasing the concentration of parathion gave significantly better control on both varieties, except from the lowest to the medium concentration on Worcester Pearmain. Although treatment E was not randomized, it seems probable that the application of the lowest concentration of parathion was more effective at commencement of egg-hatch than at petal-fall.

TABLE II.

Apple Sawfly attack data for parathion trial, 1949.

Treatment	Mean percentage fruits attacked							
	Worcester				Cox			
	Dropped	Picked	Total	Bliss transformation	Dropped	Picked	Total	Bliss transformation
A	10·0	0·02	2·5	8·7	5·8	0·5	3·8	10·6
B	31·2	0·05	12·9	20·5	13·5	1·0	9·5	17·8
C	47·4	0·43	23·9	29·1	31·4	0·7	21·0	27·1
Significant difference (P=0·05)				11·0				4·2
D	69·8	0·85	50·6	—	41·6	0·7	30·4	—
E	31·6	1·1	16·4	—	8·4	0·0	6·0	—

TRIAL WITH CHLORINATED HYDROCARBONS AND PARATHION (1950).

This was carried out in the orchard used in the 1946-48 trials (Davies and Eaton, 1950), where only Worcester Pearmain on M.IX was available. The trees were small, and each row was separated by three rows of another variety so that the chances of spray-drift were slight.

Materials.

Nicotine, employed at the usual concentration of 0·05%, was compared with seven newer insecticides, of which four had been tried by Davies and Eaton (1950) and all, except parathion, were chlorinated hydrocarbons. The identity and degree of purity of the insecticides used were as follows:

γ-BHC : 92% active ingredient(s)
Chlordane : 90% ,, ,,
DDT : 90% ,, ,,
Aldrin : 95% ,, ,,
Dieldrin : 85% ,, ,,
Toxaphene : Chlorinated camphene; chlorine content, 67-69%.
Parathion : 20% active ingredient.
Nicotine : 95-98% active ingredient.

Formulation, except in the case of parathion, which was already formulated with diacetone alcohol and a non-ionic emulsifier of the ethylene oxide condensate type, was carried out with the materials used in 1949. MB320 was employed at 0·05% and Aerosol OT at 0·01% throughout; BHC, nicotine and the lower concentration of chlordane required 0·5% diacetone alcohol, but 1·0% solvent was employed for aldrin, dieldrin, DDT, toxaphene and the higher concentration of chlordane.

Treatments.

The failure of DDT in the 1946 trial (Davies and Eaton, 1950) was not readily explicable, as this insecticide is very persistent; it was therefore retested at 0·1%. Three materials were each applied at two strengths: BHC, at 0·01 and

0·005%; chlordane, at 0·1 and 0·025%; and parathion, at 0·02 and 0·01%. Toxaphene was used at 0·1%; aldrin and dieldrin, and the nicotine standard, at 0·05%.

The treatments were randomized in seven blocks, with one tree of each treatment per block. Trees which were abnormal were not used in the main trial, but five such trees scattered in two of the blocks were used to estimate the effect of BHC at 0·01%, mixed with 1% lime-sulphur. No petal-fall fungicide was applied to any other trees in this trial.

Spraying data.

Petal-fall had progressed to 80% by 13th May and by the 17th varied from 80% to 95% in the experimental plot. Treatments were applied on the 17th with the exception of H (aldrin) and J (dieldrin) which, together with the extra treatment P (BHC plus lime-sulphur), were applied on the 18th. The temperature had fallen below 60° F. three days previously and only reached 55° and 57° F. respectively on the two spraying days. There were sunny periods on both days and no rain fell until the night of the 18th. Sprays were applied at a pressure of at least 200 lb. per sq. in., using a twin-nozzle lance directed horizontally or downwards whenever possible. Screens were used to prevent drift within the rows.

DEGREE OF CONTROL.

All dropped fruitlets as well as picked crop were collected, but only fruitlets larger than 4 mm. diameter were included in the assessment of percentage attack.

As all treatments except P were randomized, an analysis of variance was possible, and the results of this are shown in Table III where the compounds are listed in order of effectiveness. The picked crop carried a very low infestation and differences based on it between treatments were unlikely to be significant; therefore only the

TABLE III.

Degree of control of Apple Sawfly attack by various insecticides applied in 1950.

Treatment	Attack		Percentage attack (weighted)	Percentage reduction
	Mean percentage	Bliss transformation		
J. Dieldrin 0·05%	0·2	2·80	0·2	99·5
L. Parathion 0·01%	0·3	2·93	0·3	99·3
K. Parathion 0·02%	0·3	3·39	0·4	99·1
H. Aldrin 0·05%	0·5	4·00	0·5	98·9
B. γ-BHC 0·01%	0·6	4·20	0·5	98·9
A. DDT 0·1%	1·0	4·93	0·7	98·4
F. Toxaphene 0·1%	1·7	6·97	1·5	96·6
D. Chlordane 0·1%	1·8	7·27	1·6	96·3
E. Chlordane 0·025%	2·8	8·87	2·4	94·5
M. Nicotine 0·05%	2·7	9·19	2·6	94·0
C. γ-BHC 0·005%	3·1	9·56	2·8	93·6
N. Unsprayed	43·6	41·27	43·5	—
Significant differences (P=0·05)	—	3·09	—	—

total fruit figures were examined. It will be seen that all treatments, compared with unsprayed controls, gave highly significant reductions of the Sawfly attack. Nicotine, at the customary strength, gave ample commercial control in spite of the rather low temperature at spraying time and of a complete hatch of eggs. The higher concentrations of BHC and parathion gave a very high degree of control; but while the lower concentration of parathion was fully as effective as the higher, the lower concentration of BHC was significantly less effective than the higher although quite adequate for commercial purposes. DDT, aldrin, dieldrin and the higher concentration of chlordane gave excellent control. The performance of toxaphene was equal to that of chlordane at the same strength and fully adequate for commercial control; some advantages of toxaphene will be mentioned in a later section of this paper.

Phytotoxicity and compatibility of sprays.

Although success in controlling Apple Sawfly has been achieved with a variety of persistent insecticides, other properties of these materials must be considered before any recommendation can be made. The first question is whether any of these materials is likely to be phytotoxic. In the series of trials on Worcester Pearmain on M.IX reported here and by Davies and Eaton (1950), no evidence of spray damage was found. Moreover, DDT, toxaphene, aldrin and dieldrin were applied at this Station in 1950 to Cox's Orange Pippin on M.XII at 0·1% without causing leaf damage and there is no reason to expect damage by BHC or chlordane at the concentrations required for Sawfly control. In 1949, parathion caused premature yellowing and fall of primary leaves, amounting at most to 5% leaf fall, on Cox trees at this Station and at Ditton Court Farm. This leaf-fall was proportional to the concentration of parathion used, but seems to be of little significance. Parathion sprays applied to Cox trees at this Station on 19th May, 1950, did not cause any yellowing or fall of leaves, even at 0·32%. There seems little reason to suppose that the use of parathion would be accompanied by any serious risk of spray damage.

The small trial with BHC plus 1% lime-sulphur shows that no diminution of activity of this insecticide need be feared if it is applied in the first post-blossom lime-sulphur spray. It is even less likely that wettable sulphurs would interfere. Toxaphene is reported to be compatible with wettable sulphurs and there is no obvious reason to suppose it will be any less compatible with lime-sulphur than is DDT or BHC. Aldrin and dieldrin are fully compatible with lime-sulphur; unlike earlier chlorinated hydrocarbons they are stable to alkali. Parathion is known to hydrolyse fairly rapidly in alkaline materials, and is preferably applied separately from lime-sulphur, but the 1949 results show that adequate control of Apple Sawfly can be obtained when these materials are applied together.

Effects of sprays on beneficial insects.

If materials are applied for the control of Apple Sawfly at 80% petal-fall, the effect upon pollinating insects must be taken into account. Even at complete petal-fall, the presence of bloom on cover crops or weeds could lead to serious mortality among visiting bees, if the materials used were toxic to them. Little can be said about the toxicity of any of these materials toward pollinating insects other than bees, but many observations have been made regarding honey bees with all compounds except dieldrin (Hammer and Karmo, 1947; Eckert, 1949; Shaw and Butler, 1948; Todd, *et al.*, 1949; Weaver, 1949).

These workers have shown that γ-BHC and parathion constitute a real hazard to bees visiting flowers to which these insecticides have been applied, but that DDT is much safer, and toxaphene by far the safest of the materials used in the trials reported in the present paper. The application of sprays several days later than petal-fall will help to avoid injury to pollinating insects, but too long a delay could allow egg-hatch to begin before sprays were applied. The difficulty of calyx-closure on the most susceptible variety, Worcester Pearmain, also makes the earlier spraying preferable.

No direct evidence is available from these trials regarding the effect of any of these materials against predatory insects or mites. Observations made by Collyer (1953) suggest that parathion and BHC at 0·01% are toxic to an important predator of the Fruit Tree Red Spider Mite for at least a fortnight after application. However, if these insecticides are applied before 23rd May, it seems unlikely that they will persist in sufficient quantity to affect this predator which emerges throughout June and in early July.

SUMMARY.

Field trials have been conducted, on large trees in 1949 and on small trees in 1950, to compare the efficiency of new synthetic chemicals with that of nicotine for control of Apple Sawfly. A high degree of control was obtained with parathion at 0·01% to 0·02% in both years, and with six chlorinated hydrocarbon insecticides in 1950. All applications, save one, were made at petal-fall and the one egg-hatch spray applied in 1949 gave little improvement over a similar spray applied at petal-fall.

All materials tested seem to be admissible on grounds of compatibility with lime-sulphur and lack of phytotoxicity.

γ-Benzene hexachloride was very effective at 0·01% and gave commercial control at 0·005%. This insecticide, however, is very poisonous to honey-bees and probably to other pollinating insects, and applications should be left until petal-fall is complete, except perhaps on Worcester Pearmain where calyx-closure may intervene. The use of BHC in mixed orchards presents difficult problems.

Toxaphene gave commercial control at 0·1%. This insecticide is much less toxic to bees than is γ-benzene hexachloride or parathion, and could probably be applied at 80% petal-fall with very little risk to them.

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SOME FACTORS AFFECTING THE CONTROL OF APPLE SAWFLY, *HOPLOCAMPA TESTUDINEA* (KLUG), BY NICOTINE AND OTHER CHEMICALS

By **A. H. M. KIRBY** and **K. S. McKINLAY**

THE use of nicotine for control of Apple Sawfly was introduced by Petherbridge and Tunnington (1929). The failure of lead arsenate and derris as competitors of nicotine, and the success achieved in recent years with parathion and several chlorinated hydrocarbons have been discussed by Kirby and Gambrill (1953) who also obtained satisfactory control with nicotine. Nicotine has been the standard insecticide for Apple Sawfly for at least fifteen years, and it has been generally agreed that a good wetter is essential to ensure thorough wetting of the calyx-cup of the fruitlets. A good pressure will obviously help, and modern spray machines, delivering at or above 600 lb. pressure, are more than adequate for the purpose.

A number of other factors, including the mode of action of nicotine, are much less firmly established. The problem of timing sprays is not easily solved, even when nicotine is used. The original proposal of Petherbridge and Tunnington (1929) to make the first application at 7 days after petal-fall was considered by Austin, Jary and Martin (1932) to leave too large a margin for error as petal-fall is so hard to define or determine. These workers preferred to determine the peak of egg-hatch and they applied their sprays one day after this stage. But the advantage of being able to include nicotine in the first post-blossom fungicide spray which is timed for 80% petal-fall has led to this stage being accepted. The possibility of using this date, which is usually several days before egg-hatch, could hardly have been predicted, but was shown clearly by the work of Hey and Steer (1934) who obtained excellent control of Apple Sawfly when nicotine was applied to Worcester Pearmain 2 days before egg-hatch, to Cox's Orange Pippin 4 days before egg-hatch, and to Court Pendu Plat as much as 6 days before hatching commenced. The toxic effect of nicotine applied long before any larvae were about was thus established.

The control obtained by Hey and Steer (1934) exceeded that obtained by themselves or other workers with similar sprays applied after egg-hatch was well advanced, and this unexpected result called for some explanation. Hey and Steer (1934) and Steer and Thomas (1935) concluded that nicotine acted as an ovicide. In contrast, Kearns, Marsh and Martin (1936) stated that " none of the treatments showed evidence of ovicidal action although the sprays were applied eight days before egg-hatch ", and claimed that " The larvae died after consuming a portion of the calyx tissue ". (See their Table V). This conclusion could equally well have been drawn from the results of Hey and Steer (1934). Evidence will be presented in this paper showing that nicotine is not ovicidal and that the larvae die some time after hatching, presumably because, as Kearns *et al.* (1936) suggest, some of the calyx tissue has been eaten.

Miles (1932) drew attention to the possibility of the post-blossom calyx-cup closure interfering with post-blossom sprays. Failure of such sprays was attributed to this cause by Bush (1933) and by Kearns, Marsh and Martin (1935), in both cases on Worcester Pearmain. It would seem that a spray applied much after petal-fall on this variety might well fail for this reason.

There is a widespread belief that fairly high temperatures at spraying-time are necessary for effective control of Apple Sawfly with nicotine (cf. Kearns, Marsh and Pearce, 1933). The evidence to be offered from recent trials at this Station suggests that excellent control can be obtained with nicotine applied when the temperature is as low as 55° F.

1949 TRIAL.

A trial using parathion at several concentrations is reported in the preceding paper (page 163) (Kirby and Gambrill, 1953).

Ten to fifteen stung blossoms from each treatment were brought in daily and examined in order to find out at which stage in development this pest is killed. Normal development of the eggs up to eclosion took place following all treatments, and the effects of spraying only became noticeable after hatching. In blossoms taken from trees receiving the highest concentration of parathion, larvae were found dead or moribund near to or within remnants of the egg-shell. The lower concentrations of parathion failed to achieve this degree of control, larvae living for longer periods and, at the lowest concentration, sometimes succeeding in burrowing normally. A preliminary note on these observations has already been published (McKinlay, 1950).

1950 TRIAL.

In this trial several chlorinated hydrocarbon insecticides as well as parathion were compared with nicotine ; the details are given in the preceding paper (Kirby and Gambrill, 1953). Biological observations were extended to give as complete a picture as possible of egg-laying, egg-development and egg-hatching, as well as of the effect, if any, of the toxicants on the eggs.

Egg-laying.

In order to observe the rate and period of egg-laying, one branch was selected on each control tree and all the blossoms on these branches were examined daily as soon as female sawflies were observed in the orchard. The total blossoms and the number of stings were recorded ; by the time egg-laying ceased, a total of 701 blossoms had been examined and, in these, 133 stings had been found, some fruitlets bearing more than one sting. Although a percentage of stings would be unaccompanied by egg-laying, it has been assumed for convenience that the number of stings is proportionate to the number of eggs laid per tree.

The possibility that the daily handling of branches for observation might interfere with the activity of the female sawflies on them was checked by examining a total of 1,947 blossoms on eight other trees scattered throughout the experimental plot, on 12th May. This examination showed that 17·6% of these blossoms had been stung, and the same figure was obtained on the same day for the marked branches. Thus it appears that the figures obtained from the marked branches can fairly be taken as representative of the whole plot.

The figures obtained for egg-laying during the period 6th to 15th May are not inconsistent with the view that egg-laying could be represented by a curve of normal distribution with a maximum on the 11th May.

From observations made during the daily examination of blossoms, it was confirmed that the female sawfly chooses only those blossoms which are fully open and ignores buds or fruitlets which have lost their petals. A warm spell at the end of April led to 20-40% of the total blossom on trees in the experimental plot being fully open. However, a colder spell followed from 2nd to 6th May, and the first sawflies only appeared when the temperature rose again on the 7th. The earliest blossoms thus escaped stinging. As more of the early than of the later blossoms set, many of the stung fruitlets shrivelled and fell, taking the immature larvae with them ; the degree of infestation was thereby reduced, but it was considerable on the unsprayed trees. It is clear that a maximum degree of infestation will follow when the activities of sawfly and pollinating insects coincide.

Egg development.

An eighth replicated block was reserved for observations of the stages of egg development on unsprayed trees and on trees receiving nicotine, DDT, toxaphene, aldrin, dieldrin and the higher concentrations of BHC, chlordane and parathion. Twenty to thirty blossoms were examined daily from the trees receiving these eight insecticides and a further forty from a nearby unsprayed block of Worcester Pearmain; a total of 1,936 blossoms was dissected during eleven days of the developmental period. Five easily recognizable stages exist between the quiescent period following laying and eclosion of the larva :

(i) swelling of the egg with a consequent protuberance visible in the calyx cup ;

(ii) the flesh of the calyx cup over the protuberance breaks and lifts as a flap, partially exposing the egg to any spray reaching this site ;

(iii) " brown eye ", dark pigment having been laid down as the eyes form ;

(iv) movement of the larvae within the egg follows shortly after stage (iii) ;

(v) " brown mandible ", these organs becoming pigmented as they form.

It was found that the various treatments had no effect upon the rate of development, and figures for sprayed and control trees were therefore combined (Table I).

TABLE I.

Percentage of Apple Sawfly eggs reaching certain stages of development day by day in 1950.

Stage	Day in May												
	16	17	18	19	20	21	22	23	24	25	26	27	28
(i) Flap raised	24	47	69	77	—	—	—	—	—	—	—	—	—
(iii) " Brown eye " ..	—	—	—	—	67	77	97	99·5	—	—	—	—	—
(v) " Brown mandible " ..	—	—	—	—	—	—	6	43	72	88	91	93	—
Hatch	—	—	—	—	—	—	0·5	5	23	31	50	42	87

Effect of spray materials on eggs.

No larvae were found dead within the unhatched egg in blossoms taken from trees receiving any of the treatments ; all were normal and active up to the time of hatching. This confirms the 1949 observations, and indicates that none of the eight insecticides used were acting as ovicides. Differences between treatments showed up after hatching ; the percentages of larvae dead (or moribund) or active for each treatment, as recorded within 24 hours of hatching, are shown in Table II.

A striking contrast between BHC and parathion, which caused extremely rapid death of the larvae, and nicotine, which permitted larvae to survive up to 24 hours at least, is at once apparent. Of the other treatments studied in this way, only toxaphene failed to cause rapid death of larvae.

TABLE II.

Percentage Apple Sawfly larvae dead or active within 24 hours of hatching on trees receiving certain treatments in 1950.

Treatment		Percentage larvae	
		Dead	Active
DDT	0·1%	87	13
BHC	0·01%	100	Nil
Chlordane	0·1%	91	9
Toxaphene	0·1%	37	63
Aldrin	0·05%	86	14
Dieldrin	0·05%	71	29
Parathion	0·02%	100	Nil
Nicotine	0·05%	Nil	100

DISCUSSION.

Bearing of meteorological conditions.

Davies and Eaton (1950) found considerable differences in control by nicotine in the three years of their trials. Such variability in control by this insecticide is common experience and is, indeed, the *raison d'être* of these trials. Temperature records taken at this Station have been studied in relation to data for spraying-dates and 50% egg-hatch given by Davies and Eaton (1950) and Kirby and Gambrill (1953) and summarized in Table III. It is clear that the degree of control afforded by nicotine bears no direct relation to the temperature at the time of application, and that excellent control was given when the temperature on the day of application was as low as 55° C. It would seem that the explanation of variation in control by nicotine must lie elsewhere.

There is evidence, however, from the temperature records at this Station that inferior control may be linked with delayed egg-hatch due to low temperatures following nicotine application. The temperature on the day of application was about 60° F. in each year from 1946 to 1948 and lower in 1950; but it was only in 1946 that the temperature remained below 60° F. for seven days after spraying. Sharp falls in 1947 four days after spraying, and in 1950 seven days after spraying, do not seem to have delayed hatch as compared with 1948 when temperatures were generally higher. From Table III, 50% egg-hatch seems to have occurred nine days after spraying in each of the years 1947, 1948 and 1950. In 1946, however, egg-hatch was delayed, only beginning on the twelfth day and reaching 50% on the fourteenth day after the petal-fall sprays were applied. Thus the nicotine which could be supposed to be bound as a salt of one or more organic acids in the calyx tissue would have had to persist more than half as long again in 1946 as in the other years, and this degree of persistence seems not to have been achieved. In this way, adverse weather *following* spraying, sufficient to delay egg-hatch by several days, could result in poorer control by nicotine than in a year when the incubation period was shorter.

TABLE III.

Spraying temperatures and hatching-periods in the years 1946-1950.

Year	Temperature ° F.	Spraying/egg hatch period (days)	Reduction by nicotine %
1946	60	14	44·1
1947	62	9	95·9
1948	61	9	87·6
(1949)	(56)	(9)	0·0
1950	55	9	94·0

The influence of rain falling after the spray has dried is apparently slight. In the seventy-two hours after spraying, 0·20 inch was recorded in 1946, 0·81 inch in 1947, none in 1948 and 0·37 inch in 1950. It would seem unlikely that nicotine persists in a form liable to leaching, even in the presence of a good wetting-agent.

Biological factors involved.

Reference has already been made to the possible effect of a prolonged period prior to commencement of hatching, and a prolonged hatching period might also occur if the temperature falls, as sometimes occurs, late in May, after hatching has commenced. Either of these factors will extend the period from spraying to the end of egg-hatch and, hence, the period over which the insecticide must persist. In the case of the chlorinated hydrocarbon insecticides this persistence should be possible however long the period might prove.

Attention has also been drawn to the fact that, in 1950, the early blossoms set but were not stung, while the later blossoms were stung but comparatively few set. Kearns, Marsh and Martin (1935) report the same experience on Worcester Pearmain, and comment that the degree of infestation in their trial, namely 24% four days after petal-fall, " would ordinarily lead to almost complete loss of crop ", whereas in fact it had only progressed to 36% a month later. Clearly, the interaction of three factors—blossoming period, pollination period and sawfly egg-laying period—will determine whether eggs are laid in blossoms that will be shed or that will set and remain, and, hence, whether larvae will fall before migration or remain to attack other fruitlets. Control in a year such as 1950 when eggs were mostly laid in unset blossoms would be much enhanced in a year when more stung fruitlets remained until the larvae were large enough to migrate.

Mode of action of nicotine.

The idea entertained by Kearns (1933) that nicotine could kill eggs in the "brown mandible" stage of development was extended further by Hey and Steer (1934), who considered that at any stage of development the egg was susceptible to nicotine. The work of Kearns, Marsh and Martin (1936) cast grave doubts on the deductions of Hey and Steer, and the results presented in the present paper seem to confirm the view that nicotine is not ovicidal as far as Apple Sawfly eggs are concerned. That nicotine can act as an ovicide against at least one type of egg is apparent from the work of Shaw and Steer (1939) who, using the eggs of *Aphis pomi*, Deg., were able to prevent hatch with 0·1% nicotine, with sodium oleate as wetter, but not when petroleum oil-sulphite lye emulsion was used as the wetter. Evidently, the wetter makes a great deal of difference to the efficiency of nicotine in this case. It is well to bear in mind that Hey and Steer (1934) employed sodium oleate for the trial where nicotine was effective when applied six days before egg-hatch, and the possibility does remain that nicotine may be ovicidal for Apple Sawfly eggs if a suitable wetter, such as sodium oleate, is used, but it is not a probability. The weight of evidence now favours the view that nicotine acts as a stomach poison to the larvae of this pest as soon as they commence to bore.

The absence of ovicidal action was also apparent with the other spray materials used in 1950. But, particularly with BHC and parathion and, in lesser degrees, with the other insecticides (Table II), larvae died very soon after eclosion, being found in some cases within the remnants of the egg-shell. There is thus no need to postulate any fixation of these materials in the calyx-tissue; it is enough to assume that persistant deposits remained on the egg-shell and on the surface of the calyx.

SUMMARY.

The influence of weather conditions upon the degree of control of Apple Sawfly obtained with nicotine in trials at this Station has been studied for the years 1946-48 and 1950. Nicotine was fully effective in 1947 and in 1950 when the temperatures on the day of application of sprays were 62° F. and 55° F. respectively, whereas poor control was obtained in 1946 when the spraying temperature was 60° F. From these data it is concluded that the temperature on the day of spraying is not a factor in control by nicotine, but a study of the maximum temperatures during the period following spraying and up to egg-hatch in each year suggests that a cool period subsequent to spraying may delay egg-hatch beyond the period for which sufficient nicotine may persist.

The effects of the interaction of blossoming period, pollination period and sawfly egg-laying period are discussed, and data provided for the latter and also egg-development in 1950.

The development and eclosion of eggs subjected to the various treatments was followed in 1949 and 1950. No ovicidal action could be seen following any of the sprays in either year. It is concluded that nicotine, at least in the presence of most wetters, does not act as an ovicide upon Apple Sawfly eggs, and the same conclusion seems valid for the potential substitutes. Evidence points to a stomach-poison action of nicotine, but the other materials listed in Table II seem to act upon the larva mainly or entirely by contact action.

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It is a pleasure to acknowledge assistance in recording from our colleague, Mr. R. G. Gambrill.

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SPECIFICATION OF RADIANT FLUX AND RADIANT FLUX DENSITY IN IRRADIATION OF PLANTS WITH ARTIFICIAL LIGHT*

Communication of the Committee on Plant Irradiation of the "Nederlandse Stichting voor Verlichtingskunde"† (Secretariat: Utrechtseweg 210, Arnhem, The Netherlands)

In modern biology a number of influences of radiation on living matter are known. When speaking about radiation, we consider only infra-red, visible and ultra-violet radiation. Several practical applications have resulted from our knowledge of these influences.

One of the earliest applications was ultra-violet therapy. Another example is the artificial irradiation of plants, which now has general application in horticulture. A survey of the many investigations in the sphere of plant irradiation shows that the irradiation applied is not always adequately specified and that the comparison of results is hindered by the use of different units. Furthermore, the practice of plant irradiation needs a method of evaluating a light source for irradiation purposes, even if only approximately.

For these reasons the Committee for Plant Irradiation, established by the Netherlands Illumination Foundation, thinks it desirable that a system for the specification of the radiant intensities and the light sources should be generally accepted as soon as possible. Such a system is proposed for discussion in this paper.

THE UNITS LUMEN AND LUX.

Before outlining a method for the specification and measurement of the radiation in plant irradiation, we may refer in this section to current practice in lighting engineering.

Each source of radiation consumes a quantity of energy per unit of time and releases the same power. The power consumed is transformed into:

1. a quantity of heat per unit of time; this heat is lost by conduction and by convection;
2. a quantity of radiation per unit of time, emitted in all directions, i.e. a radiant flux.

The *radiant flux* is characterized by its quality (spectral distribution of energy, and its quantity (intensity). The spectral energy distribution is denoted by the quantity of radiation as a function of the wavelength. The radiant energy per unit of time can be expressed in watts, the unit of power (=energy/sec) in the international system of electrical units. Other units, in which the radiant energy can be expressed, are the calorie and the erg. 1 watt=0·239 cal/sec=10^7 erg/sec. The wavelength is expressed here in millimicrons (mμ), which unit we prefer to the Ångström unit (Å). 1 mμ=10^{-9} meters=10 Å.

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† To be referred to as: Comm. Plant Irradiation Ned. St. Verl. The membership of the committee during the preparation of this communication was as follows: Prof. Dr. E. C. Wassink, chairman; Dr. G. A. W. Rutgers, secretary; Dr. Ir. E. W. B. v.d. Muyzenberg, Dr. J. W. M. Roodenburg, Miss Dra Chr. v.d. Scheer, Dr. J. B. Thomas, Dr. R. v.d. Veen, Dr. J. Voogd and Prof. Dr. Ir. S. J. Wellensiek, members.

The lighting engineer is particularly interested in radiation in the visible spectral region, which extends from about 400 to 700 mμ. The problem to him is to determine the visual effect of the radiation on the human eye. The quantitative value of a radiant flux for illumination purposes is therefore determined by a corresponding *luminous flux*, which is connected with the radiant flux in the following way.

A certain quantity of radiant energy in the red and blue spectral region contributes less to the visual impression than the same quantity of energy in the green spectral region. This is a result of the sensitivity of the eye, which is a function of the wavelength of the incident radiation. The spectral sensitivity is quantitatively expressed by the international luminosity curve. This curve was adopted by the International Commission on Illumination in 1924 (C.I.E., 1924) and is represented in Fig. 1, where the relative luminosity factor V_λ of the standard light-adapted eye is plotted as a function of the wavelength λ. V_λ is nearly zero at a wavelength of 400 mμ, then increases with increasing wavelength to its maximum value 1 at 555 mμ and decreases again until nearly zero at a wavelength of 700 mμ. The contribution of the radiation of a given wavelength to the luminous flux is determined by the value of V_λ at that wavelength. With the aid of the concept luminous flux, other concepts and units have been developed, which are very useful in illumination practice.

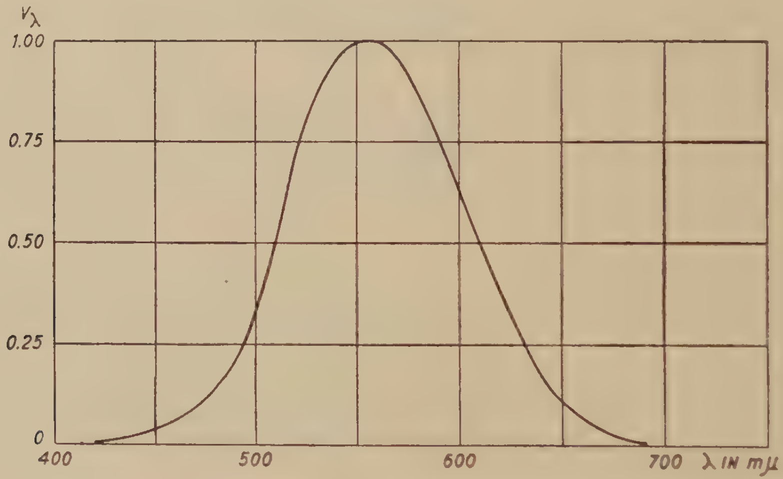

FIG. 1.
Relative luminosity factor V_λ as a function of the wavelength λ.

A luminous flux is expressed in lumens. A lumen is the luminous flux emitted in a solid angle of one steradian by a uniform point light-source having an intensity of one candela (before 1948 : candle. Cf. Ned. St. Verl., 1941).

Originally the candle was defined with the aid of standard carbon filament lamps, operated under accurately prescribed conditions. In 1937 the International Committee on Weights and Measures replaced the international candle and the derived units by a new system of units, which is based upon the radiation of a black body (full radiator). According to this new definition, the luminous flux emitted per steradian by a square centimeter of a black body at the point of solidification of platinum amounts to 60 lumens ; the luminous intensity of one square centimeter of the black body under these conditions is 60 candela (cd). By these definitions the photometric units are related to the physical units.

At a wavelength of 555 mμ a radiant flux of 1 watt corresponds to a luminous flux of about 680 lumens. For an arbitrary wavelength the luminous flux, corresponding to a radiant flux of 1 watt, is obtained by multiplying 680 by the relative luminosity factor V_λ at the wavelength under consideration. If a radiant flux consists of radiation of different wavelengths, one has to multiply the radiant flux (in watts) of each wavelength by the corresponding 680 V_λ and to add the products. The sum represents the luminous flux corresponding to the entire radiant flux.

The value of the luminous flux emitted by light-sources used for illumination purposes, readily gives an indication to the illuminating engineer as to whether a lamp is suitable for a certain illumination project.

In practice he has to illuminate objects and for this purpose it is adequate to introduce the concept *illumination.* For a homogeneously illuminated surface, the illumination is the luminous flux per unit of area. The unit of illumination is the *lux,* which represents an illumination of one lumen per square meter.

From the foregoing it follows that *both the lumen and the lux are based upon the international luminosity factor.*

PLANTS AND RADIATION.

Irradiation of a plant produces a number of physiological effects. (Cf. Roodenburg, 1940, 1950.) One is particularly interested in irradiation with wavelengths of the visible, the near infra-red and the ultra-violet region. As arbitrary limits one can take wavelengths of 300 mμ in the ultra-violet and 1,000 mμ in the infra-red. Radiation with a wavelength shorter than 300 mμ tends to produce an irreversible destruction of the tissue. The principal effect of irradiation with a wavelength greater than 1,000 mμ is to raise the temperature of the plant and it may be said, provisionally, that no specific action of that radiation occurs.

The fundamental effect of radiation upon plants is photo-synthesis. In 1883 T. W. Engelman found that for green plants the photosynthetic activity of red and blue radiation is greater than that of green radiation.

This is confirmed by the spectral curve of photosynthesis determined by Hoover (1937) and reproduced in Fig. 2. Since this curve was measured for wheat, it cannot be expected to be valid under all circumstances of plant irradiation. The effect of plant irradiation is determined by the absorption factor of the plant for radiation of different wavelengths. This factor depends not only on the spectral absorption factors of the absorbing pigments, but also on the thickness of the absorbing layer.

A thin layer of chlorophyll absorbs red and blue radiation more strongly than yellow and green radiation. In thick layers, e.g. in thick leaves or in plants with a thick foliage, these differences may be considerably reduced (Rabideau *et al.* 1946).

In addition to photosynthesis, several other effects of radiation upon plants are known. Phototropism, that is to say the curvature of plants in response to unilateral

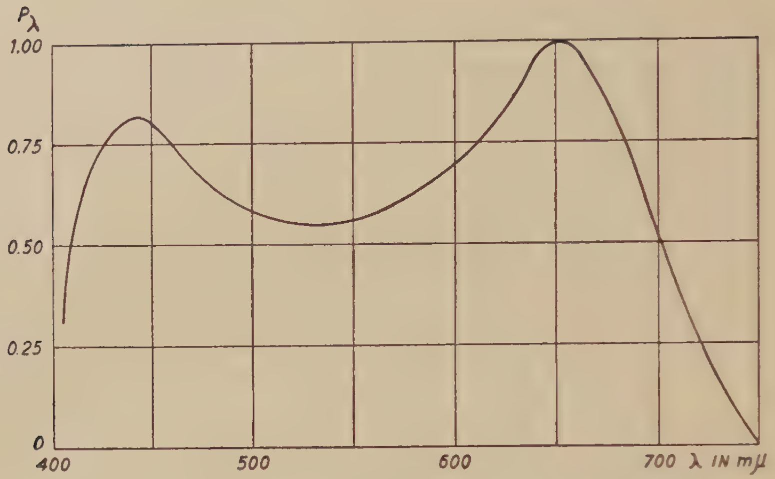

FIG. 2.
Spectral photosynthetic effectiveness P_λ as a function of the wavelength λ for wheat (Hoover, 1937).

illumination is, according to Blaauw (1909), mainly caused by the blue-violet radiation. The light-absorbing pigment is probably yellow.

Important effects of radiation upon plants are concerned with day-length, for instance the promotion or suppression of flower formation by increasing the duration of the irradiation. Most of the practical applications of plant irradiation are performed with a view to this purpose. The colour of the light, with which the day-length is increased, is important. In several cases red radiation has been found to be most effective (Borthwick *et al.*, 1946, 1948, 1950).

The near infra-red radiation may produce a specific elongating effect (Roodenburg, 1940). The limits of the spectral region in which this effect occurs are not known but it is probable that it extends from 700 to 1,000 mμ (Roodenburg, 1947, Wassink *et al.*, 1950, 1951). Other formative effects of radiation upon plants are especially produced by blue radiation. Other effects of radiation upon plants are of greater or less importance.

It is evident from the above, that important effects of radiation on plants are due to visible radiation. Consequently, the same concepts and units are often used in plant irradiation and in illuminating engineering. In particular, the luminous flux with the lumen as unit and the illumination with the lux as unit are often applied. Obviously, it is unreasonable to characterize the efficiency of a light source for plant irradiation by the value of its luminous flux.

If, for instance, a neon lamp, a mercury vapour lamp and an incandescent lamp have the same luminous flux, the last source emits much more near infra-red radiation than the others. Owing to the elongating effect of that radiation, the incandescent lamp will be unsuitable in certain cases. The mercury vapour lamp, on the other hand, emits relatively more blue-violet radiation than the other two sources and therefore produces certain formative effects. Furthermore, the photosynthetic effectiveness of the three sources may be different.

Consequently the luminous output of a lamp is no good measure of its effectiveness in plant irradiation. On the contrary, values for the luminous flux and the illumination will only be confusing in an attempt to evaluate an installation for plant irradiation according to the photometric concepts mentioned.

This committee is of the opinion that the use, in plant irradiation, of the photometric units lumen and lux is a practice which must be strongly deprecated.

This advice leads on to the possibility of defining for plant irradiation concepts, analogous to those in lighting practice, with the aid of one or more specific sensitivity curves, even if such curves in plant irradiation are only approximately valid. The illuminating engineer is aware that the international luminosity curve accounts only partially for the spectral activity of radiation in producing a luminous effect. But notwithstanding this deficiency, the use of the luminosity curve and the units based upon it has proved to be very useful in lighting practice. The main reason for this is that the international luminosity curve is sufficiently valid for most individual cases.

A similar method was proposed in the application of ultra-violet radiation, which led to the definition of specific biological units of radiation. With the aid of an erythema curve a unit for the erythemal effectiveness of the radiant flux, the viton, was introduced. Based upon a germicidal curve, a unit for the germicidal radiant flux has been proposed. However, unlike the lumen and the lux, these units have not been generally adopted, because the spectral activity curves, upon which they are based, are not considered sufficiently representative for all individual cases.

Undoubtedly the same argument is valid in plant irradiation. In many photobiological processes the site of action of the radiation is in the leaves. These differ from plant to plant, in the important specific absorptions as well as in their thickness and in the number above each other. Consequently, the quantitative properties of the spectral sensitivity curves of the foliage of different plants may vary considerably. As explained above, the photo-biological processes, occurring in the leaves, have diverging sensitivity curves. Furthermore the specific sensitivity of the different plants for each of these processes is different and finally, the sensitivity of the plants for each of the processes can be very different. It follows that in applying a certain illumination to different species of plants, the reactions can be different depending on the preponderance of one photo-biological process over the others. Further, the influence of the dark-metabolism will not be the same in different species or in the same species under different circumstances.

This committee, therefore, considers that the use of specific units adapted for plant irradiation should be discouraged. The use of the spectral sensitivity curves would be very limited under the widely divergent conditions of plant irradiation.

A PROPOSAL FOR THE SPECIFICATION OF RADIANT FLUX AND RADIANT FLUX DENSITY IN PLANT IRRADIATION.

The total radiation of a light source may be characterized by the total radiant flux in watts and by a diagram which represents quantitatively the distribution of the radiation over the spectrum. In the same way the radiant flux density (or irradiance) can be characterized by the total radiant flux density expressed, for instance, in watts per square meter, and the spectral energy distribution of the radiation.

In practice this method cannot be recommended because of the difficulty of surveying the data. Furthermore, important deviations in the far infra-red can be expected for some lamp-types, depending upon the operation conditions. Our committee therefore proposes to separate the total spectral region into a number of bands, as has been done in photometry (Bouma, 1937). The limits of these bands should be chosen to fulfil the purposes of plant irradiation. We propose to characterize lamps for plant irradiation by the values of the radiant flux in each of the spectral bands. The irradiance can be specified in an analogous way by means of the radiant flux density in each spectral band.

The following spectral bands are suggested :

1st band : *radiation with a wavelength longer than 1,000 mμ.* No specific effects of this radiation upon plants are known. It is acceptable that this radiation, as far as it is absorbed by the plant, is transformed into heat without the interference of biochemical processes.

2nd band : *radiation between 1,000 mμ and 720 mμ.* This is the region of the specific elongating effect upon plants. Although the spectral region of the elongating effect does not coincide precisely with the limits of this band, one may provisionally accept that the radiant flux in this band is an adequate measure of the elongating activity of the radiation.

3rd band : *radiation between 720 mμ and 610 mμ.* This is almost the spectral region of the strongest absorption of chlorophyll and of the strongest photosynthetic activity in the red region. In many cases it also shows the strongest photoperiodic activity.

4th band : *radiation between 610 mμ and 510 mμ.* This is a spectral region of low photosynthetic effectiveness in the green and of weak formative activity.

5th band : *radiation between 510 mμ and 400 mμ.* This is virtually the region of strong chlorophyll absorption and absorption by yellow pigments. It is also a region of strong photosynthetic activity in the blue-violet and of strong formative effects.

For the sake of completeness one can add to these divisions a classification of the ultra-violet radiation, proposed by Coblentz (C.I.E., 1939). For plant irradiation this classification is less important.

6th band : *radiation between 400 mμ and 315 mμ (ultra-violet A).*
7th band : *radiation between 315 mμ and 280 mμ (ultra-violet B).*
8th band : *radiation with wavelengths shorter than 280 mμ (ultra-violet C).*

In order to apply these specifications in horticultural practice, it is necessary to know the total gross wattage and the power consumed by the auxiliary equipment of the lamps available commercially ; the difference of these two quantities is equal to the power consumed by the lamp (net wattage). Furthermore, the distribution of the net wattage over the spectral bands must be known. As an example the distribution of energy over the spectral bands for some lamps is given in Table I.

As for the irradiance, the committee is of the opinion that this quantity also must be expressed in energy units. In the practice of artificial plant irradiation this can be easily achieved if sources are used with known spectral distribution of energy.

Table I.

Percentage of gross watts in the spectral bands.

	Incandescent (tungsten filament) lamp (220V)	High pressure mercury vapour HO 2,000	High pressure mercury vapour HP 80W	Sodium SO 85W	Fluorescent daylight TL 40W
Gross watts	500	475	83	106	49
Lamp watts	500	450	75	85	40
Longer than 1,000 mμ (approx.)	60	60	40	30	30
Between 1,000 and 720 mμ	13·6	0·9	2·0	0·6	0·0
Between 720 and 610 mμ	4·3	0·3	0·7	0·2	2·9
Between 610 and 510 mμ	2·3	6·5	5·6	12·6	5·5
Between 510 and 400 mμ	0·9	3·3	4·1	0·02	5·8
Shorter than 400 mμ	0·13	0·8	4·6	0·02	0·4

Each instrument used for the measurement of the irradiance must then be calibrated for the radiation of a certain lamp-type ; then the reading of the instrument for the total radiation is, at the same time, a measure of the contribution of each spectral band to the irradiance produced by the lamp under consideration.

The committee considers, further, that a suitable unit of irradiance should be defined. This is made difficult by the fact that the most obvious unit, viz., the watt per square meter, is already used in installations for plant irradiation, to indicate the total power installed per square meter. This power is only partly used for the irradiation of the surface under consideration. Furthermore the order of magnitude of the watt per square meter is not suitable for all applications.

This committee therefore proposes to introduce as a unit of irradiance *the milliwatt per square meter* (mW/m^2), which has the advantage of equalling the erg per square centimeter per second (erg/cm^2sec).

We consider it necessary to introduce a separate name for this unit of irradiance and propose the term " *sol* ".

SUMMARY.

The present communication deals with some proposals of the Dutch Committee on Plant Irradiation for the specification of the radiation of light sources used in installations for irradiation of plants with artificial light.

The committee draws attention to the fact that the units lumen and lux, which are used with advantage in illuminating engineering, have no meaning when applied to the irradiation of plants.

To characterize the light sources, which are used in installations for plant irradiation, it is proposed to distinguish a number of spectral bands. The biological meaning of the limits of these bands is indicated. The quantity of radiation in each band can be expressed in milliwatts per square meter ; for this unit the name " sol " is proposed.

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STUDIES IN IRON DEFICIENCY OF CROPS

II. THE INTERRELATIONSHIPS OF IRON AND POTASSIUM IN THE POTATO PLANT

By E. J. HEWITT and E. W. BOLLE-JONES*
Agricultural Research Council Unit of Plant Nutrition (Micronutrient elements)
Long Ashton Research Station, University of Bristol

A GENERAL discussion of the problems of iron deficiency by Wallace and Hewitt (32) included evidence that iron and potassium are interrelated in plant metabolism.

Several references (4), (5), (6), (7), (8), (9), (11), (18), (24), (31), (32), (34) to incidental observations relevant to the problem have been recorded during work not specifically intended to examine this relationship.

The relation between potassium and efficiency of iron utilization by soybeans may be genetically controlled (35). The inefficient genotype which was chlorotic in calcareous soils, contained less " soluble " iron, more total iron and a lower potassium content. Total potassium was significantly greater in efficient genotypes. Pineapple (27) or alfalfa leaves (30) grown at high potassium levels contained more iron than did those grown at low levels. Potassium deficiency also caused a localized deposition of insoluble iron compounds at the nodes of maize plants (1), (15). In some instances the addition of potassium reduced the iron content in leaves of sugar cane and in pasture plants (2), (12), (13), (29).

Potassium supply affected the ratio of chlorophyll A to B in sugar beet and potato (37) and potassium was also thought to increase chlorophyll production by facilitating the movement of iron from roots to leaves (26).

This paper describes experiments carried out in sand culture with the potato in 1945, 1946 and 1947 to examine the interrelationship of iron and potassium. The potato was chosen because (*a*) it shows well-defined symptoms of both iron and potassium deficiencies, (*b*) both elements were thought to be concerned in the blackening of tubers on boiling (33) and (*c*) it is of economic importance.

EXPERIMENTAL.

METHODS.

The experiments included limited combinations of different levels of iron, potassium and phosphorus. The lowest level for each (Fe_1, K_1 or P_1) represented moderate or acute deficiency, the middle level (Fe_2, K_2 or P_2) was adequate or only slightly deficient, and the highest (Fe_3, K_3 or P_3) was probably in excess of the plants' requirements.

The different levels expressed as milliequivalents per litre (m.eq./L.) in the nutrient solution used, together with the concentrations of other nutrients, are given in Table I.

The nutrients were purified from iron by the phosphate adsorption method (28) modified to include sodium bicarbonate for greater efficiency (14). Sodium phosphate was used in the 1945-6 experiments. Potassium phosphate was also used in 1947, so that 0·08 m.eq./L. of potassium, i.e. equal to the K_1 level, was present in the diluted nutrient when ready for application. The amount of phosphate retained in the purified nutrient for the P_1 cultures, was negligible.

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* Now at The Rubber Research Institute, Kuala Lumpur, Malaya.

Rainwater purified by passage through Permutit resins (14) was used in all the experiments. The residual iron levels in Fe_1 solutions before application were 0·05 p.p.m. (1945), 0·02 p.p.m. (1946) and 0·005 p.p.m. (1947). No ferric citrate, therefore, was added to the Fe_1 nutrients. Different levels of potassium and phosphorus were compensated with sodium (1·33–6·33 m.eq.) and sulphate (3·3-6·3 m.eq./L.) ; calcium was kept constant. Micronutrients were given at normal concentrations (14).

TABLE I.

Nutrient concentrations in terms of milliequivalents/litre.

Year	Fe_1	Fe_2	Fe_3	K_1	K_2	K_3	P_1	P_2	P_3
1945	0·002	0·27	1·07	0·0	3·3	6·6	0·0	4·0	7·0
1946	0·001	0·30	0·90	0·0	3·3	6·6	0·0	4·0	7·0
1947	0·0003	0·30	1·50	0·08	0·8	8·0	4·0	4·0	4·0

Mg 3·0 ; Ca 6·8, 1945-46 ; 8·0, 1947. NO_3 10·1, 1945-46 ; 13·0, 1947.

The sand purification technique and modifications during the period considered have been described (14). The quality of the purified sand improved each year.

In 1945 and 1946 the K_1P_1 cultures received 1 litre of solution containing K_2 and P_2 levels as " starters " before planting. The respective solutions were used from the beginning in 1947.

The potato variety was Majestic, of certified Scotch seed stock. Tubers were sprouted and were planted three inches deep either in April (1945-6) or May (1947) in 10-inch clay pots treated with wax or bitumen paint.

" Young " (partly expanded) and " old " (mid-stem) leaves were sampled at intervals. These regions were visually most sensitive to the different levels of iron and potassium supply. The tubers were harvested in August (1945, 1947) or in October (1946) and weighed fresh. The petioles were extracted with Morgan's reagent and tested for " soluble " iron, potassium, phosphorus and calcium (19), (22). Total chemical analysis was carried out in 1947 on powdered dried leaves, including petioles, after digestion with nitric and perchloric acids.

Iron was determined with αα-dipyridyl (36). Potassium was precipitated as the cobaltinitrite (3) and the cobalt fraction determined colorimetrically as thiocyanate (10). Phosphate was determined by a molybdenum blue method (16), slightly modified. Calcium was precipitated as the oxalate and was estimated volumetrically with permanganate. Manganese was determined by the periodate method (23) modified to include phosphoric acid (20).

RESULTS.

VISUAL OBSERVATIONS.

An important feature of the results was the visual behaviour of plants in different treatments.

At Fe_1K_1 levels, plants were stunted and pale green. Apical leaves soon developed acute yellow or ivory chlorosis and old leaves showed typical potassium deficiency necrosis and scorch in pale leaves. These symptoms also occurred in the Fe_1K_2 treatment in 1947 when only 0·8 m.eq./L. K^+ was given. Triangular buff-coloured necrotic areas appeared adjacent to the midrib in the upper chlorotic leaflets of Fe_1K_1 plants in 1947. The necrosis was rare in Fe_1K_2 plants and was absent from all other treatments.

At normal or high potassium levels (K_2-K_3) in the Fe_1 series, growth was greatly increased and plants were vigorous. Apical leaves were normal but middle and old leaves were pale or yellow green, but free from symptoms of potassium deficiency.

The supply of iron also determined the incidence of potassium deficiency. Thus plants grown at the Fe_1K_1 level were the first to show potassium deficiency in the old leaves. Progressive increase in iron supply (Fe_2-Fe_3) consistently *delayed* the appearance of symptoms by 5-10 days for each increment of iron ; all foliage was a dark bluish-green. In Fe_1K_1 plants, breakdown of older leaves progressed slowly up the axis but apical growth continued normally. At Fe_2 and Fe_3K_1 levels, the middle and finally the young leaves were more severely scorched and death of the growing point often occurred, followed by regeneration from basal axillary shoots.

Effects of limited variation of phosphorus level were not marked. High iron or potassium levels accentuated phosphorus deficiency and high phosphorus levels correspondingly affected incipient iron or potassium deficiencies.

GROWTH.

Increased iron supply decreased the height of stems, shown in Table II, for most treatments in the 1945-46 experiments. In 1947 increased iron increased the height when potassium was deficient but slightly reduced it when adequate potassium was given. The differences between 1945-46 and 1947 may have reflected improved sand purification. The effect of increased phosphorus supply was to increase the height at the Fe_2 and Fe_3 levels and sometimes to reduce it at the Fe_1 level.

Yield figures are presented in Table II. In 1947 the lowered yields were attributed to harvesting at an earlier growth stage and, at the lower iron levels, to improved sand purification.

Increase of potassium at any iron level increased the tuber yields (with one exception, at the Fe_1 level in 1946). Increase of iron at any potassium level increased both total and tuber yield in the 1947 experiment. In the 1945 and 1946 experiments, however, the effect was limited to the K_1 level ; effects at K_2 and K_3 levels were complex. Increasing phosphorus from P_1 to P_2 increased tuber yield. Further increase from P_2 to P_3 depressed the yield at Fe_1 and usually increased it at Fe_2 and Fe_3 levels. The average weight of tuber increased with potassium supply. Increased iron supply from Fe_1 to Fe_2 increased the average weight of tuber ; further increase to the Fe_3 level gave a further rise in 1947 but generally depressed it in 1945 and 1946.

TABLE II.

Average height of plants (cm.) ; crop weights (g. per pot) and average weights of tubers.

Year	Fe level		K and P level				
			K_1P_2	K_2P_2	K_3P_2	K_2P_1	K_2P_3
1945	Fe_1	Height	71	76	76	—	81
		Tuber yield ..	144	869	1,134	—	721
		Average weight ..	11·2	39·5	54·1	—	38·0
	Fe_2	Height	41	51	56	31	56
		Tuber yield ..	147	448	751	153	472
		Average weight ..	22·1	49·7	75·1	21·9	49·7
	Fe_3	Height	31	51	58	18	53
		Tuber yield ..	172	549	601	108	493
		Average weight ..	19·2	38·3	51·5	12·0	49·3
1946	Fe_1	Height	55	66	45	36	53
		Tuber yield ..	50·0	568	563	23·3	537
		Average weight ..	4·6	42·6	60·3	2·5	39·3
	Fe_2	Height	35	52	59	20	76
		Tuber yield ..	66·0	603	772	56·7	797
		Average weight ..	11·0	60·3	105	9·0	104
	Fe_3	Height	25	45	45	9	52
		Tuber yield ..	76·0	533	670	91·7	617
		Average weight ..	12·0	76·2	74·4	27·5	63·8
1947	Fe_1	Height	28	47	99		
		Tuber yield ..	2·4	14·6	87·2		
		Average weight ..	4·8*	2·0	6·7		
	Fe_2	Height	42	61	92		
		Tuber yield ..	24·5	91·5	336		
		Average weight ..	4·6	7·8	18·3		
	Fe_3	Height	45	56	90		
		Tuber yield ..	37·1	120	392		
		Average weight ..	9·3	16·0	30·0		

* In this treatment 5 tubers were produced from 10 pots and their total weight was 24g.

" SOLUBLE " NUTRIENTS IN TISSUE EXTRACTS.

As values for the 1945-46 experiments were assessed on the Low (L), Medium (M), High (H) nomenclature (21), only general trends could be noted. 1947 data were assessed quantitatively by standards and are given in Table III. On the basis of the three years' results, the following general conclusions seemed justified.

1. Increased potassium supply increased the " soluble " potassium and decreased the calcium ; its effect on " soluble " iron content was not always clear but on balance there was evidence of a slight increase.

2. Increased iron supply tended to increase the " soluble " iron content and to decrease the potassium, calcium and phosphorus.

TABLE III.

" Soluble " Fe, K and Ca and old/young leaf ratios for potato in 1947 experiment.

Treatment		K level											
		K_1				K_2				K_3			
Fe levels	Leaf sampled	HCl extract p.p.m. Fe	" Morgan's " extract p.p.m. Fe	K	Ca	HCl extract p.p.m. Fe	" Morgan's " extract p.p.m. Fe	K	Ca	HCl extract p.p.m. Fe	" Morgan's " extract p.p.m. Fe	K	Ca
	Date 9/7/47												
Fe_1	Old leaf	0·8	0·3	10	400	1·0	0·3	60	—	1·0	0·3	200	200
	Young leaf	0·8	0·2	200	275	0·6	0·2	250	275	0·4	0·3	300	10
	Ratio	1·0	1·5	0·05	1·5	1·7	1·5	0·24	—	2·5	1·0	0·7	20·0
Fe_2	Old leaf	1·2	0·4	30	275	1·8	0·4	50	275	1·4	0·6	50	100
	Young leaf	0·4	0·2	150	275	0·8	0·4	200	180	3·0	0·3	250	10
	Ratio	3·0	2·0	0·2	1·0	2·2	1·0	0·25	1·5	0·45	2·0	0·2	10·0
Fe_3	Old leaf	1·4	0·4	100	300	2·0	0·6	40	300	2·0	0·6	250	50
	Young leaf	0·8	0·3	30	180	2·4	0·4	50	<10	3·0	0·8	250	10
	Ratio	1·8	1·3	3·3	1·7	0·8	1·5	0·8	>30	0·7	0·75	1·0	5·0
	Date 5/8/47												
Fe_1	Old leaf	4·0	1·0	15	250	4·0	1·2	25	225	4·0	1·6	250	200
	Young leaf	2·0	0·2	150	150	4·0	0·3	200	200	0·8	0·4	400	Nil
	Ratio	2·0	5·0	0·1	1·7	1·0	4·0	0·13	1·1	5·0	4·0	0·6	>20
Fe_2	Old leaf	0·8	1·0	10	300	0·6	2·0	15	250	0·6	1·8	300	75
	Young leaf	2·0	0·4	25	200	0·6	0·5	50	275	0·6	0·8	150	Nil
	Ratio	0·4	2·5	0·25	1·5	1·0	4·0	0·3	0·9	1·0	2·25	2·0	>7·5
Fe_3	Old leaf	0·8	2·0	10	250	0·6	1·6	20	200	0·6	2·0	300	Nil
	Young leaf	2·0	0·5	10	150	0·6	0·5	75	75	0·6	1·0	250	Nil
	Ratio	0·4	4·0	1·0	1·7	1·0	3·2	0·26	2·6	1·0	2·0	1·2	about 1

The ratios for old and young leaves of "soluble" iron, potassium and calcium for the 1947 experiments are also given in Table III. At the first sampling, the acid extracts of old leaves usually contained more iron than did those of young leaves at the low Fe and low or medium K levels, but there was an opposite trend at the higher levels (Fe_3K_2, Fe_2K_3, Fe_3K_3). At the later sampling the Morgan's reagent extracts of old leaves consistently contained more iron than did those of the young, but the iron extracted by HCl showed less consistent behaviour.

The old leaves generally contained less soluble potassium than did the young. But there was a marked increase in the ratio (old/young) with increased iron supply at the K_1 level and less, but generally consistent increases, at the K_2 and K_3 levels. This ratio, with one exception (Fe_2K_2) also increased with increased potassium supply.

The old leaves contained more calcium than did the young; at the higher K levels, the old/young ratio for calcium tended to be high.

TOTAL NUTRIENTS IN DRY MATTER.

The results obtained in 1947 are presented in Table IV.

Increased supplies of potassium increased the potassium content. At the K_1 and K_2 levels, increased iron supply tended to decrease the potassium content, especially in the young leaves. At the K_3 level increased iron supply increased the potassium content. Increased supplies of potassium decreased the iron content of the young leaves at the Fe_1 level, whereas at the Fe_2 and Fe_3 levels the iron content increased. The trends for the old leaves were inconsistent. The phosphorus content diminished with increased supplies of either iron or potassium, more markedly in the old leaves with potassium, and in the young leaves with iron increments. Calcium contents decreased regularly with increased iron supply (with one exception). Increase of potassium from K_1 to the K_2 level invariably increased the calcium content; further increase from K_2 to K_3 decreased it. The manganese content of the young leaves increased with increased potassium supply; in the old leaves manganese varied inversely with the iron content as the potassium supply increased.

The old to young leaf ratios of total nutrient content in dry matter are also given in Table IV. With the exception of the Fe_1K_1 treatment the old leaves contained slightly more iron than the young leaves and the old/young iron ratio showed surprisingly little variation. The old leaves contained less potassium than the young, except for treatments Fe_3K_2 and Fe_3K_3 where it was the reverse. The ratio of old/young potassium increased regularly with increased iron supply.

With increased potassium supply the ratio of phosphorus in old/young leaves declined whereas increased iron supply consistently increased this ratio. Increased potassium supply was found generally to increase the old/young ratio for calcium content; a similar but less consistent tendency was observed for increased iron supply.

DISCUSSION.

Some of the experiments reported here were incomplete in design for statistical purposes; replication was limited and did not permit of tests of significance. Despite these shortcomings, however, certain well-marked responses were consistently obtained. The absence of chlorosis and general vigour of the Fe_1K_3 plants

PLATE I.

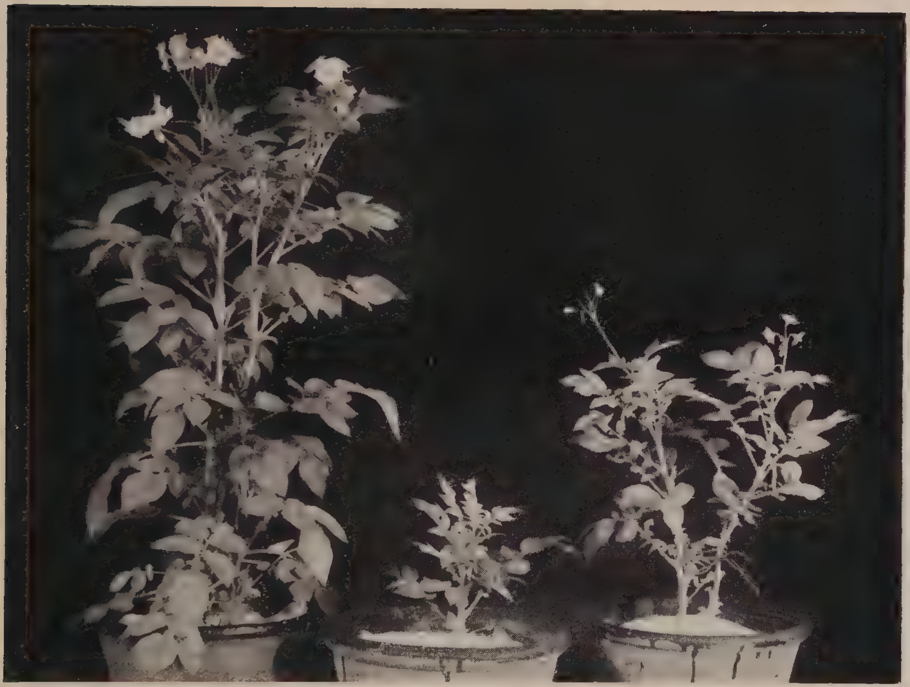

FIG. 1.
Potato experiment, 1947.

Left: High potassium—low iron(Fe_1K_3). *Centre and Right:* Low and Medium potassium—low iron (Fe_1K_1 and Fe_1K_2).

Note apical chlorosis in K_1 and K_2 treatments and simultaneous potassium deficiency scorch of lower leaves. In the K_3 treatment the young leaves are greener than the older leaves.

TABLE IV.

Mineral composition of dry matter (sampled 15/8/47) and old/young leaf ratios.

Treatment		K level														
Fe level	Leaf sampled	K_1					K_2					K_3				
		p.p.m. Fe	p.p.m. Mn	%K	%P	%Ca	p.p.m. Fe	p.p.m. Mn	%K	%P	%Ca	p.p.m. Fe	p.p.m. Mn	%K	%P	%Ca
Fe$_1$	Old leaf	114	519	0·49	0·76	4·59	250	214	0·68	0·54	5·25	153	340	4·17	0·25	4·76
	Young leaf	264	388	2·69	1·33	8·94	194	444	3·27	1·20	3·39	113	482	7·39	1·00	1·26
	Ratio	0·43	1·34	0·18	0·57	0·51	1·29	0·48	0·21	0·45	1·55	1·35	0·71	0·56	0·25	3·78
Fe$_2$	Old leaf	159	240	0·30	0·59	3·60	167	54	0·47	0·51	4·08	147	444	5·84	0·23	3·05
	Young leaf	118	89·2	1·01	0·78	1·55	135	170	1·91	0·88	1·59	130	230	4·98	0·77	1·15
	Ratio	1·35	2·69	0·30	0·76	2·32	1·24	0·32	0·25	0·58	2·57	1·13	1·93	1·17	0·30	2·65
Fe$_3$	Old leaf	228	250	0·58	0·58	2·43	190	256	0·47	0·42	3·55	264	1,097	6·72	0·30	2·39
	Young leaf	162	194	1·20	0·71	1·17	171	215	1·71	0·70	2·31	177	283	5·17	0·60	0·80
	Ratio	1·41	1·29	0·48	0·82	2·08	1·11	1·19	0·28	0·60	1·54	1·49	3·88	1·30	0·50	2·99

as compared with the Fe_1K_1 $(-K_2)$ plants that showed acute apical chlorosis, suggested that a limited amount of iron was apparently more readily available or more favourably distributed for growth and chlorophyll formation in the presence of ample potassium.

The " soluble " iron results suggested that enhanced potassium status might have increased the " active " iron as related to chlorophyll synthesis. The possibility that additional supplies of potassium salts merely carried in more iron as an impurity was examined and found to be unlikely. Subsequent work (by E.W.B-J.) has completely dispelled this possibility as a factor in these results. The seasonal trend in extractable iron also supported the suggestion (17) that the proportion of iron effective in chlorophyll formation might decrease with age. The mechanism of such changes is still obscure. Early work with maize (15) and results by one of us (E.J.H.) (32) with oats show that other crops may be similarly affected. On the other hand, unpublished work by E. W. Bolle-Jones (1948) indicated that clover, sugar beet and tomato were not particularly sensitive to the relationship. Increased potassium intake may stimulate organic acid production (E.W.B-J., unpublished). Plants with high tissue pH values often have abnormally low " soluble " iron and high total iron contents (25) (35).

Increased acidity might thus enhance the " active " iron fraction either directly or by complex formation. It is hoped that investigations in progress will throw further light on this aspect of the problem.

The visual effects and beneficial growth responses induced by increased potassium supply at low iron levels were always accompanied by decreased phosphorus content. It seems probable that one effect of increased potassium was to diminish phosphorus content of the foliage, as found also in alfalfa (30), and thereby to increase the availability of iron within the plant. High iron supply could also induce symptoms of phosphorus deficiency which became more severe with increased iron level. In the 1946 experiment, high potassium supplies induced mild phosphorus deficiency at the Fe_3 level, while high phosphorus supply induced potassium deficiency at the same iron level. This point will be considered in detail in a later paper.

Not only did potassium supply influence iron status but, conversely, iron supply appeared to affect the distribution of potassium. The consistent *increase* in the old/young leaf ratio for total (and usually " soluble ") potassium with increased iron supply might imply that iron, especially in the high iron—low potassium treatments, impeded the full utilization of the potassium present or restricted the translocation of potassium from old to young leaves when present in inadequate amounts. This would account for the *earlier* appearance of first symptoms of potassium deficiency in the Fe_1 series, and for the more drastic breakdown of younger leaves at a later stage in the Fe_3 series compared with continued apical growth observed in Fe_1K_1 plants. The mechanism of the reciprocal effects of iron and potassium on their distribution and relative " activity " and their effect on growth, composition and water relations of the leaf will be the subject of further work.

SUMMARY.

1. Potato plants (variety Majestic) were grown in sand culture in 1945-47 at deficiency, normal and excess levels of iron, potassium and phosphorus.

2. Visual observations showed a reciprocal relationship between iron and

potassium. Deficiency of potassium accentuated deficiency of iron. Increased potassium supply decreased apical chlorosis and produced vigorous, pale green plants.

3. At the lowest potassium level, plants in all iron treatments showed severe potassium deficiency symptoms. These commenced in the older leaves, appeared first in the low iron treatments and were *delayed* in appearance by increased iron supply.

Increased iron concentration, however, increased the ultimate severity of the potassium deficiency symptoms, especially in the apical regions.

4. Phosphorus deficiency appeared at the lowest phosphate level and was accentuated by increased iron or potassium supply.

5. Yields and average weight of tubers increased with potassium. Iron and phosphorus produced complex effects.

6. Increased potassium increased (*a*) " soluble " and total potassium contents of the leaves, (*b*) the old/young leaf ratio of " soluble " potassium.

7. Increased iron usually decreased the " soluble " and total potassium in young leaves and increased the old/young leaf ratios for " soluble " and total potassium.

8. Extra potassium generally increased iron content at the higher iron levels ; at the lowest iron level it decreased it in young and increased it in old leaves.

9. Total phosphorus content diminished with increased potassium or iron ; calcium content decreased with increased iron supply. Extra potassium first increased, then decreased calcium in the leaves.

10. The results support the idea that iron and potassium are interrelated in the metabolism of the potato plant. Potassium may enhance iron utilization and iron may impede translocation of potassium.

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SPRAYING EXPERIMENTS AGAINST APPLE AND PEAR SCAB AT LONG ASHTON AND IN THE WEST MIDLANDS, SEASON 1951

By H. E. CROXALL* and J. E. E. JENKINS†
N.A.A.S. Plant Pathology Laboratory, Evesham
and
R. J. W. BYRDE and R. W. MARSH
Long Ashton Research Station, University of Bristol

THE experiments described in this paper form a continuation of those carried out at Long Ashton in 1949 and 1950 (Byrde and Marsh, 1951). Materials showing promise in these earlier trials were further tested at Long Ashton in 1951 while, with the support of the Agricultural Research Council, arrangements with the N.A.A.S. were made for more extensive trials, planned by Dr. Croxall, to be carried out in commercial plantations in the West Midlands. To facilitate the comparison of results, both sets of trials are reported in this joint paper.

DESCRIPTION OF CENTRES.

Trials on apples.

Long Ashton. The varieties used were Cox's Orange Pippin, Worcester Pearmain, Lane's Prince Albert and Stirling Castle. The trees, planted in 1935, were in grass, regularly cut by a gang-mower, and were spaced at 21 ft., except the Worcesters, which were at 15 ft. Particulars of treatments, replications and spraying dates are included in Tables I, II and III.

Holt Heath, Worcestershire. This 4-acre plantation was planted in 1921 at 10×10 ft., later thinned to 20×10 ft. Tree vigour was low but reasonably even within each variety. The trees were in rough grass which in 1951 was left uncut until mid-August. Details of the treatments on Worcester Pearmain are given in Table IV. The other varieties included, and the respective sprays applied, were :

Cox's Pomona and Cox's O.P.—lime-sulphur.

Bramley's Seedling and Stirling Castle—lime-sulphur, ziram.‡

Newton Wonder—heptadecyl glyoxalidine, soluble organo-mercury sulphonate.§

Lane's P.A.—thiram||, ziram, lime-sulphur, soluble organo-mercury sulphonate, heptadecyl glyoxalidine, mixed glyoxalidines**.

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* Now at N.A.A.S. Provincial Headquarters, Elswick Hall, Newcastle-upon-Tyne.
† Now at N.A.A.S. Laboratory, Cheshunt, Herts.
‡ Zinc dimethyldithiocarbamate.
§ See footnote to Table I.
|| Tetramethylthiuram disulphide.
** See footnote to Table IV.

Tillington, Herefordshire. This was a vigorous, well-managed 5-acre block of 40-year-old trees, seeded down to grass, and spaced at 18 ft. square. Each of the following treatments was twice replicated on the three varieties, Bramley, Worcester and Grenadier: heptadecyl glyoxalidine, mixed glyoxalidines, and soluble organo-mercury sulphonate. Both of the glyoxalidine sprays were applied on 20th April (green cluster), 27th April, 11th May (pink bud), 1st June (petal fall) and 13th June (fruitlet). The mercury spray was applied on 20th April and 11th May only, these blocks being subsequently sprayed with 1% lime-sulphur on 1st June and 13th June. All blocks received a lead arsenate spray (2 lb./100 gal.) on 28th June.

Trials on pears.

Long Ashton. The pears used were two 25-tree rows, one of Williams' Bon Chrétien and the other of Doyenné du Comice, planted at 15 ft. in 1925 but with many replacements. Details of treatments are given in Table VII.

Barton, near Bidford, Warwickshire. This was a 5-acre block of ten 70-tree rows of Doyenné du Comice (with a few interplanted Conference and Pitmaston Duchess) standing at 15×10 ft. The trees were 30 years old and of moderate vigour. Following a winter cultivation in 1950-51, they remained in tumble-down grass and weeds through the summer. The middle strip (70×5 trees) was sprayed four times in 1951 with mixed glyoxalidines; the eastern flanking strip (70×3 trees) and the western strip (70×2 trees) were left unsprayed throughout. Dates of application are given in Table VIII.

FACTORS AFFECTING INTENSITY OF SCAB ATTACK.

Levels of shoot infection in March, 1951.

At Long Ashton there was a moderately high level of shoot infection following the wet summer of 1950. At Tillington, Bramley and Grenadier showed the usual freedom from shoot infection and little was seen on Worcester. In contrast, Worcester and Cox at Holt Heath showed abundant shoot infection: no observations were made here on the other varieties.

On the Comice pears at Barton, the distribution of scabbed wood was very uneven. The exposed western side of the block was much more lightly infected than the sheltered eastern rows. At the northern end, which lay wet during the winter, scab infection of shoots reached a remarkably high level, about a quarter of the leaders being killed by the fungus. The intensity of attack gradually diminished towards the south and west of the block.

Weather.

Compared with the 1914-48 means, the rainfall of 1951 was above normal in April, May and August, equal to normal in September, and below in June and July. The monthly totals at Long Ashton were (in inches): April 3·80, May 2·94, June 0·68, July 1·66, August 5·10, September 3·02. At Holt Heath the corresponding figures were: 2·35, 2·51, 0·67, 1·12, 3·30, 1·83.

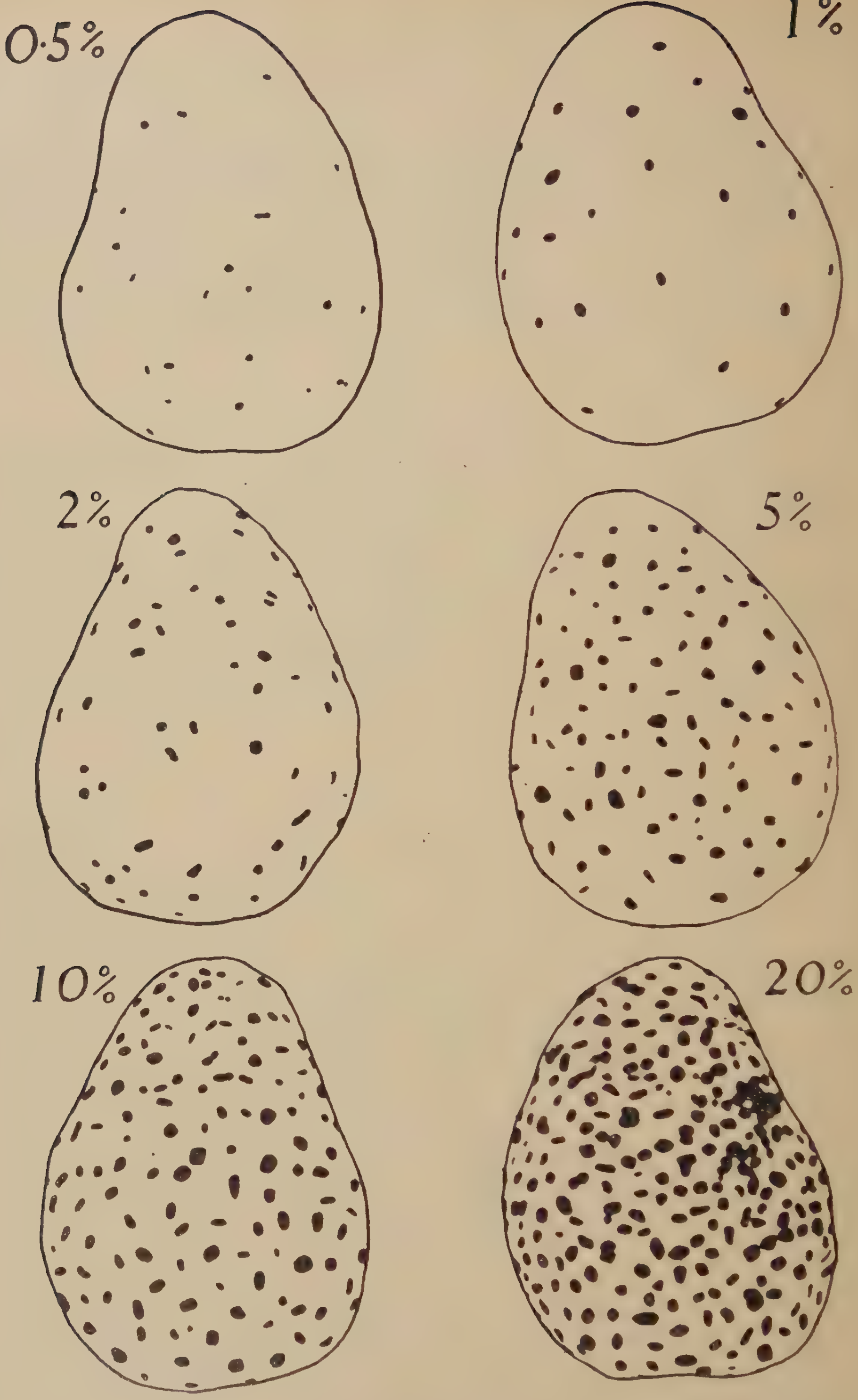

Fig. 1.
Scale for estimating percentage scabbed area on pear fruits. (In each example the spotting continues uniformly over the whole surface of the fruit.)

Spraying equipment and methods of recording.

Spraying equipment.

At Long Ashton a small mobile sprayer was used, with a single-nozzle broom (disc 5/64 in. aperture; pressure 75 lb./sq. in.).

The sprays at Holt Heath were applied, through the kind co-operation of the Worcestershire Agricultural Executive Committee, with the Committee's power sprayer employing manually-operated spray lances.

Both at Tillington and in the pear plantation at Barton the spraying was done by the grower's spray team using power sprayers. At Barton, automatic spraying with fixed booms was employed for all applications.

Methods of recording.

Mean percentage scab areas per leaf and per fruit were assessed by Tehon and Stout's method as amplified by Marsh (1947). The samples taken comprised at least 250 leaves or 100 fruits per tree, picked from a cone-shaped space extending to the centre of the tree from the north side. For the assessment of scab on pear fruits, where infection occurred as numerous small spots scattered over the fruit surface, models were prepared showing 0·5, 1, 2, 5, 10 and 20% infection of the total area. (See Text-fig. 1.)

RESULTS (APPLES).

Scab control.

Long Ashton: Worcester.

Table I.

Worcester at Long Ashton (Exp. A5). Sprayed 11th May, 4th June and 4th July. Four replicates of one-tree treatments.

Spray material	Concentration	Mean % area scabbed	
		Leaves (9th Aug.)	Fruits (23rd Aug.)
Ziram (80%)	0·3%	0·04	0·02
Lime sulphur	2% then 1%	0·20	0·03
Thiram (80%)	0·3%	0·13	0·07
Phenyl mercury acetate (2½% Hg)	0·002% Hg	0·58	0·30
Soluble organo-mercury sulphonate* (0·8% Hg)	0·002% Hg	0·64	0·26
Phenyl mercury chloride (2½%)	0·002% Hg	0·59	0·26
Chlorphenyl sulphide†	0·1%	1·33	0·45
Control		1·64	0·78
Significant difference at *P*=0·05		0·44	0·12

Bracketed values are not significantly different.

* Di-phenyl mercuric salt of di-2:2′-naphthylmethane-3:3′-disulphonic acid.

† *Bis* (5-chloro-2-hydroxyphenyl) sulphide.

TABLE II.

Worcester at Long Ashton (Exp. A2). Sprayed 7th May, 5th June and 3rd July. Nine replicates of one-tree treatments.

Spray material	Concentration	Mean % area scabbed	
		Leaves (14th Aug.)	Fruits* (27th Aug.)
Phthalimide† (50%)	0·2%	0·11	0·07
Lime-sulphur	2% then 1%	0·38	0·34
Control		0·95	0·80
Significant difference at $P=0·05$		0·17	0·17

* On a sample of 50 fruits per tree.

† *N*-trichloromethylthiotetrahydrophthalimide.

Long Ashton : Cox.

TABLE III.

Cox at Long Ashton (Exp. A1). Sprays applied 3rd May, 5th June and 14th-16th July : 6-tree blocks, twice replicated.

Spray material	Concentration	Mean % area scabbed
		Fruits (27th Sept.)
Heptadecyl glyoxalidine (34%)	0·375%*	0·45
Lime-sulphur	2% then 1%	0·49
Control	—	1·01

* Plus 8 oz. hydrated lime per 100 gal. wash.

The mean values for lime-sulphur and heptadecyl glyoxalidine are both significantly lower than that for control, but do not differ significantly from each other.

Holt Heath : Worcester.

The full range of fungicide treatments at this centre was applied only to the Worcesters and the scab control counts were made on this variety only. Samples were taken from four equidistantly spaced trees in each of the eight half-rows. The results are listed in Table IV.

There was significantly less leaf scab on all sprayed plots than on the controls ; significantly less on the plot sprayed with mixed glyoxalidines than on those sprayed with ziram or with heptadecyl glyoxalidine ; and significantly less on the lime-sulphur plot than on the ziram or the heptadecyl glyoxalidine plot. The fruit counts showed significantly less scab on the ziram plot than on the heptadecyl

TABLE IV.

Worcester at Holt Heath. Sprays applied 3rd May, 5th June, 27th June.

Spray material	Concentration	Mean % area scabbed	
		Leaves (8th Aug.)	Fruits (30th Aug.)
Ziram (50%)	0·3%	0·65	0·17
Lime-sulphur	2% then 1%	0·30	0·25
Mixed glyoxalidines† (50%)	0·25%*	0·27	0·26
Thiram (20%)	0·3%	0·57	0·36
Soluble organo-mercury sulphonate	0·002 then 0·001% Hg	0·60	0·39
Heptadecyl glyoxalidine (34%) ..	0·375%*	0·70	0·46
Control 1	—	2·43	2·27
Control 2	—	2·75	2·20

* Plus 8 oz. hydrated lime per 100 gal. wash.

† A mixture of glyoxalidine acetates containing 32% of the 2-heptadecyl derivative, 16% of the 2-pentadecyl and 2% of the 2-heptadecenyl.

glyoxalidine plot, and significantly less on all treatments than on controls. The lay-out of the plot did not allow of an estimate of the separate effects of site and treatment in giving these results. The only evidence on the effect of site is that the figures from the two controls showed no significant difference.

Tillington : Bramley, Worcester, Grenadier.

The heavy programme of applications at this centre gave an almost complete control of scab on all plots, and no counts were made.

PHYTOTOXICITY.

Long Ashton : Lane's, Stirling, Cox.

As in previous years (Byrde and Marsh, 1951) phytotoxicity was assessed numerically by counts on the sprayed trees.

TABLE V.

Mean numbers of fruit per tree following fungicide treatments.

Treatment	Variety		
	Lane (26th Sept.)	Stirling (4th Sept.)	Cox (27th Sept.)
Phthalimide	448	364	not tested
Heptadecyl glyoxalidine	441	222	710
Lime-sulphur	not tested	not tested	763
Control	455	341	569

Long Ashton : Worcester.

Records were made of the numbers of russeted unscabbed fruits noted in picking the crop in Experiments A2 and A5. Results are given in Table VI.

TABLE VI.

Russeting of unscabbed fruits of Worcester Pearmain following fungicide treatments.

Exp.	Treatment	Unscabbed fruits	
		Total	No. russeted
A 2	Phthalimide	398	14
	Lime sulphur	244	17
	Control	76	7
A 5	Chlorophenyl sulphide	77	8
	Soluble mercury sulphonate	107	11
	Phenyl mercury chloride	134	7
	Phenyl mercury acetate	125	4
	Thiram	182	29
	Ziram	193	41
	Lime sulphur	195	12
	Control	55	0

The high russeting figure following treatment with ziram is noteworthy.

Holt Heath : Worcester.

In picking the fruit, arbitrary figures were allotted for skin colour as follows : high colour (completely red), 4 ; moderate colour (two-thirds red), 3 ; poor colour (two-thirds green), 2 ; very poor colour (completely green), 1. On this basis the mean colour index was as follows :

Control—4·0.
Thiram: soluble organo-mercury sulphonate: mixed glyoxalidines—3·0.
Lime-sulphur—2·5.
Ziram—2·0.
Heptadecyl glyoxalidine—1·5.

No serious spray damage was noted on any variety in the Holt Heath plantation, but a slight leaf mottling occurred on leaves of Newton Wonder sprayed with the soluble organo-mercury preparation, and slight russet was noted on Stirling fruits sprayed with ziram.

Tillington : Grenadier, Bramley and Worcester.

No numerical data on phytotoxicity were obtained at this centre, but in mid-August leaf mottling was obvious on all trees sprayed with the soluble organo-mercury followed by lime-sulphur. No adverse effect on yield was apparent.

RESULTS (PEARS).

SCAB CONTROL.

Long Ashton : Williams'.

The crop harvested was extremely light, so the fruits for each treatment were bulked and the scab assessed on the totals.

TABLE VII.

Results on Williams' at Long Ashton. Sprays applied 24th April, 21st May, 11th-12th June: 8 replicates of one-tree treatments.

Spray material	Concentration	Percentage fruit area scabbed (20th Aug.)
Phthalimide spray (50%)	0·2%	0·36
Heptadecyl glyoxalidine (34%)	0·375%	1·33
Control	—	4·53

The crop on the Comice trees was negligible, and no assessment of scab was possible.

Barton: Doyenné du Comice.

As noted earlier, the initial infection of this plot showed wide variation. Assessments were therefore made in the 14th, 28th, 42nd, and 56th rows (from N. to S.) and in each of these rows the second, fifth, sixth and ninth tree (from W. to E.) was recorded. This gave one tree in the western control strip, two in the sprayed strip and one in the eastern control strip for each of the rows selected. The leaf results, obtained on 9th August, and the fruit results (17th October) are set out in Table VIII to show the effect of position in the plot.

TABLE VIII.

Results on Comice at Barton. Sprays applied 19th April, 5th May, 23rd May, 8th June.

NORTH

		Unsprayed	Sprayed		Unsprayed	
		Tree 2	Tree 5	Tree 6	Tree 9	
WEST	A. Mean percentage leaf area scabbed					EAST
	Row 14	0·85	0·06	0·02	3·59	
	Row 28	0·25	0·00	0·08	1·24	
	Row 42	0·62	0·04	0·14	2·04	
	Row 56	0·22	0·02	0·08	1·34	
	B. Mean percentage fruit area scabbed					
	Row 14	6·90	2·46	1·49	5·45	
	Row 28	6·49	2·79	3·67	6·58	
	Row 42	6·16	2·52	1·74	5·65	
	Row 56	9·49	2·09	1·36	5·31	

SOUTH

C. Treatment means	Leaf	Fruit
Sprayed	0·06	2·26
Unsprayed	1·27	6·50
Significant difference ($P=0{\cdot}05$) ..	0·76	1·16

PHYTOTOXICITY.

No numerical data were obtained on phytotoxicity of sprays to pears. At Barton, the glyoxalidine spray caused some bronzing of foliage, erratically distributed through the sprayed block, but this had no apparent effect on vigour or cropping. Certain of the interplanted trees of Conference, particularly at the northern end of the plantation, showed a "swan-neck" malformation of the leaves followed by premature defoliation. This phenomenon occurred on both sprayed and unsprayed trees but appeared to be accentuated by the spray treatment.

DISCUSSION.

APPLE TRIALS.

In any comparison of the results of the above trials on apples, it should be noted that at Long Ashton the level of fruit infection on the unsprayed Worcester was less than half that at Holt Heath. Although the Holt Heath summer rainfall was lower, the initial reservoir of infection, the crowded trees and their undergrowth of long grass provided almost ideal conditions for incubating apple scab. At Long Ashton (Exp. A5), counts on fruit scab ranked treatments in the following descending order : ziram, lime-sulphur, thiram, organo-mercurials—the results for the first three being not significantly different. At Holt Heath, although all the levels of infection were higher, it is noteworthy that the corresponding counts ranked these treatments in the same order ; although here the lay-out did not permit a statistical examination of treatment results. As the thiram concentrate used at Holt contained only 20% active ingredient, the fungicidal performance of both the ziram and the thiram sprays in these trials was of a high order.

One of the Long Ashton trials, however, gave marked russeting of Worcester following the use of thiram and (particularly) ziram. Previous records by Montgomery, Moore and Steer (1942) emphasize the variability of past fungicidal trials with thiram.

The phenyl-mercury sprays showed, in the Long Ashton trial, a significantly poorer performance than lime-sulphur, but it must be emphasized that they were used at a mercury concentration of 0·002%, whereas phenyl mercury chloride sprays are usually employed at approximately double this strength. Although the three mercurials employed differed markedly in solubility, they showed almost identical fungicidal performance in the field, suggesting that the eradicant fungicidal effect of the organo-mercurials is of greater importance than their protectant action. The low concentrations of organo-mercurials used in these trials induced no phytotoxic effects except leaf mottling, but it should be noted that the experiments did not include the use of mercury sprays on trees of Cox's Orange Pippin.

The newer glyoxalidine formulation (heptadecyl glyoxalidine) controlled apple scab on Cox at Long Ashton to the same degree as the standard lime-sulphur treatment, and was non-damaging to Cox and Lane. At Holt Heath, the plot sprayed with heptadecyl glyoxalidine showed markedly more scab than that treated with the mixed glyoxalidines, but the significance of this treatment effect cannot be assessed. Fruits of Worcester Pearmain sprayed with heptadecyl glyoxalidine at Holt were inferior in colour to those sprayed with the mixed glyoxalidines. More extensive results are needed before the relative merits, under English conditions, of the two glyoxalidine preparations can be assessed.

The result of the pilot trial made with the phthalimide spray confirmed that of the previous year in demonstrating that this material was significantly more effective in apple scab control than the standard lime-sulphur sprays. In the trials for phytotoxicity so far made, the phthalimide preparation has caused no injury to Lane or Stirling.

PEAR TRIALS.

At Long Ashton, the limited data obtained on Williams' pears indicated that the fungicidal performance of the phthalimide spray on this variety was better than that of heptadecyl glyoxalidine.

Previous trials at Long Ashton having proved the value of the mixed glyoxalidines on the pear variety Comice, the main 1951 trial on pears was made in a commercial Comice plantation which had hitherto been unproductive because of either scab or spray damage. In this trial, the assessment made in early August showed that leaf infection on the plots sprayed with mixed glyoxalidines was one-twentieth of that on the unsprayed plots. This wide difference was not preserved on the fruits, which in the ensuing two months of heavy rainfall showed much late scab infection. The sprayed plots were exposed to unusually high risk of attack through being flanked by the heavily-infected control strips. Even so, the mid-October infection on the plots treated with glyoxalidine up to June was only one-third of that on the unsprayed trees.

The mixed glyoxalidines, although not entirely non-damaging in this trial, caused no injury of economic importance on Comice. Further experiments are necessary to establish the effect on pears of the heptadecyl glyoxalidine and of the phthalimide preparation.

SUMMARY.

On Worcester Pearmain apples at Long Ashton in 1951, three applications of the thiocarbamate sprays, ziram (at 0·24%) or thiram (at 0·24%), gave a control of Apple Scab equal to that following the standard lime-sulphur programme (2% pre-blossom and 1% post-blossom). Fruit russeting was increased by the thiocarbamates. Three organo-mercury preparations, each used at 0·002% Hg, gave equal scab control, but these preparations were less effective than the standard lime-sulphur. The above results were paralleled in a non-replicated trial in Worcestershire made under conditions specially favourable to Apple Scab infection.

A 0·125% heptadecyl glyoxalidine spray equalled lime-sulphur in Apple Scab control but showed no advantage over 0·125% mixed glyoxalidines.

A preparation of 0·1% trichloromethylthiotetrahydrophthalimide surpassed lime-sulphur in Apple Scab control and showed no phytotoxicity in trials at Long Ashton on Worcester Pearmain, Lane's Prince Albert and Stirling Castle.

In a heavily-infected plantation of Doyenné du Comice pears in Warwickshire, four applications of the 0·125% mixed glyoxalidines reduced fruit infection to one-third of that on the unsprayed blocks and caused no damage to the crop.

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SOME FACTORS AFFECTING FLOWER PRODUCTION IN THE TOMATO

By D. LEWIS

John Innes Horticultural Institution, Bayfordbury, Hertford, Herts

DESPITE the extensive research which has been done on the physiology of the tomato plant there has been little on the factors affecting flower production. Went (1945) reports for the tomato that " the size of the inflorescence varied very much with night temperature ; the warmer the night, the smaller the inflorescence and the flowers. Fruit set went parallel with flower development. Only at 22° [C.] and 13° [C.] night temperature did fruit start to grow ; at higher temperatures no fruit was set at all." Dorland and Went (1947) report for the Chili pepper that the lower the night temperature the more buds develop into flowers.

Mather (1948) has reported that plants of tomato grown outdoors have a larger number of flowers than plants grown in a greenhouse.

The experiments to be described were undertaken not as a physiological study but because the number of flowers in tomatoes is ideal material for a genetic study of a character which is polygenically determined and which is influenced by environmental differences that can be easily controlled. But although the main object of the work was a study of gene-environment interaction, some physiological experiments were necessary before the genetical experiments could be planned. To delay the publication until the genetical work had matured was considered undesirable because of the possible importance of the results for practical tomato culture. From the physiological point of view there are several aspects of this work which are incomplete.

BRANCHING OF THE INFLORESCENCE.

The inflorescence of most tomato varieties is a simple or little branched raceme of a varying number of flowers : this type has been called " simple ". In a few varieties such as Wonder of Italy the inflorescence is large and much branched and has been called " compound ". The simple type of inflorescence is due to a gene **S** which is completely dominant, Crane (1915). In the present experiments all the plants used had the simple inflorescence and were homozygous, **SS**.

The range in number of flowers per inflorescence among the varieties with the simple type is given in the appendix by Crane and Brown. From this it is evident that the number of flowers varies over a fairly wide range.

The degree of branching among the simple types is also not constant. It may vary from a single stem to two, three or more branches. Nevertheless the most branched simple type is quite distinct from the true recessive compound type which has as many as fifty branches and 300 flowers.

The relationship between number of flowers and the degree of branching is shown in Table I. This gives the results of a test of different conditions during seedling growth and their effect on the number of flowers in Vetomold and Kondine

TABLE I.

A comparison between the number of flowers and the type of branching of the first inflorescence in two tomato varieties and under two conditions of seedling growth (greenhouse and cold frame).

Variety		Vetomold								Kondine Red							
Condition ..		Greenhouse				Frame				Greenhouse				Frame			
No. of inflorescence branches		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
No. of plants		60	3	1	—	44	17	3	—	26	37	1	—	11	32	19	2
No. of flowers per inflorescence	Min.	5	13	18		6	12	19		9	15	25		9	15	25	39
	Max.	9	15			9	16			14	25			13	30	35	45
Mean no. of flowers per inflorescence ..		7·65*	8·11† ± 0·84			8·11*	9·94† ± 0·84			11·6*	16·14† ± 0·84			11·6*	21·62† ± 0·84		

* Mean of unbranched inflorescences. † Mean of all inflorescences.

Red. These varieties were chosen because they had the lowest and highest number of flowers respectively, among the varieties which had been counted.

The seeds were sown at 26° C. in an incubator on the 14th April, 1949. Ten days later the seedlings were transferred to a greenhouse at approximately 22° C. Four days later the seedlings were potted: half of each variety was left in the greenhouse and a half was transferred to a cold frame. The light intensities in the greenhouse and frame were approximately the same but the temperature of the cold frame was always lower, often by as much as 10° C., than that of the greenhouse. The plants were planted outside in 4 latin squares on 7th June. The rather extensive results of this experiment will not be given because others, to be described later, deal more precisely with all the points except the relationship between branching and number of flowers.

The following conclusions on the branching of the inflorescence can be drawn from the data in Table I.:

1. There is a positive correlation between number of flowers and the degree of branching.

2. There is a distinct range of flower number for each type of branched inflorescence.

3. A comparison between the mean numbers under the two conditions shows that in Vetomold, if the unbranched inflorescences are taken alone in the calculation of the mean number of flowers, the effect of the two conditions on the mean is still present. It is apparent from this that an increase in number of flowers by the cool conditions is not an indirect effect of the induction of branched inflorescences but that the general level of flower initiation is raised and this in turn results in more branched inflorescences. Kondine Red does not show the treatment difference in the means of the unbranched inflorescences. This does not indicate, however, that there is any fundamental difference between the two varieties, but that in Kondine Red the number of unbranched inflorescences is a much smaller proportion of the whole and thus they would not be expected to show the same difference on the mean.

The distinct range of flower number in each type of branching can have a misleading effect when the distribution frequencies of inflorescences with different flower numbers are plotted. The distribution is frequently bimodal as shown in Fig. 1. As both the strains of Vetomold and Kondine Red are inbred, it would be unlikely that this bimodality could be due to segregating genes controlling the number of flowers. The bimodality is in fact due to the difference between the unbranched and branched inflorescences. The first peak is the mode of flower number of the unbranched and the second peak of the branched inflorescences. One other feature of the distribution curves is the sharper peak obtained with the plants grown under cool frame conditions. This is to be expected if we consider that the cool condition primarily effects flower initiation and that branching is a secondary effect of greater flower production. Under the cool conditions there should be a piling up of maximum numbers for an unbranched inflorescence, and then a sharp drop in the frequency before the threshold for a branched inflorescence is reached.

Although the relationship between branching, total number of flowers and environment is an important physiological study, it was not carried further in the experiments owing to the already complex nature of the main problem, the interaction of genotype and environment. In all later experiments the number of flowers has been taken as the criterion of inflorescence size.

TEMPERATURE AND INFLORESCENCE SIZE.

The first test of the effect of temperature on flower production was made on the variety Ailsa Craig. Seeds were sown on 21st March, 1947 in two constant temperature cabinets, one at 26±0·2° C., the other at 13±0·2° C. The cabinets were of glass on 5 sides and were placed in a greenhouse. When the seedlings had produced their first true leaf they were transplanted into pots. The time taken to attain this transplanting stage varied from 10 to 21 days according to the sowing temperatures. At the time of transplanting, the seedlings of each germination treatment were divided at random into 2 groups. One group of each treatment was placed in a warm greenhouse and the other group in a cold frame. The temperatures in these two environments were not controlled, but the greenhouse was kept as warm as possible and the frames were unheated. The soil conditions in the greenhouse and frame were identical, the light intensities were comparable but were slightly higher in the frame during the incidence of direct sunlight.

The results of the test are given in Table II. The most striking difference in flower number is between the plants in the greenhouse and frame. The low temperature of the frame has resulted in significantly more flowers than the higher temperatures of the greenhouse. A slight, but statistically significant difference in flower number is caused by the germination temperatures but these differences are too small to be of any practical importance. In view, however, of this slight effect seedlings were germinated in later experiments at a constant temperature of 26° C.

TABLE II.

Mean number of flowers in the first inflorescences in the tomato variety Ailsa Craig under different conditions of germination and two different conditions of growth from the time of cotyledon expansion.

Germination temp. (°C.)		Greenhouse	Cold frame
Day	Night		
26	26	9·02±0·15	11·02±0·33
26	13	9·42±0·05	11·24±0·35
13	26	9·47±0·04	12·79±0·45
13	13	9·22±0·18	10·51±0·31

Table III gives the results for three years when the varieties Kondine Red and Vetomold were grown in a warm greenhouse and cold frame. Very marked differences in flower number were found in 1949 and 1951, the frame-raised plants producing more flowers. In these years the difference between greenhouse and frame temperatures was great. But in 1950 the seed sowing had to be delayed until 24th May, and at this time the cold frame was frequently as warm as the greenhouse. This is reflected in the small difference obtained in flower number in that year. In 1951 plants from three single plant selections were used.

TABLE III.

Mean number of flowers in the first inflorescence under greenhouse and frame conditions during the years 1949-1951.

	Kondine Red		Vetomold	
Year	Greenhouse	Cold frame	Greenhouse	Cold frame
1949	16·1±·8	21·6± ·8	8·1±·8	9·9±·8
1950	12·4±·8	14·0± ·9	6·9±·3	6·8±·3
1951*	12·6±·5	28·1±1·4	7·1±·3	12·1±·6
	12·5±·6	31·4±1·8	7·2±·3	12·7±·5
	13·8±·6	32·6±1·9	6·5±·2	14·5±·6

* The three sets of figures for each variety in 1951 were from three different single plant selections.

To avoid the fluctuations in temperature which are present in the greenhouse and frame, plants were grown in 1951 in controlled temperature rooms which were illuminated solely by artificial light from 5 ft. 80-watt fluorescent tubes. The tubes were 2 in. apart and were of the Osram Daylight and Osram Warmwhite types alternating. The lights were 2 ft. above the plants, giving approximately 1,000 foot candles at plant level. The light period was 14 hours, and relative humidity 60-75%. The plants used were an F_2 generation from a cross between Kondine Red and Vetomold. The results were: at 12° C., 13·62 flowers per first inflorescence and, at 25° C., 7·83 flowers. Thus, for a 13° rise in temperature, the number of flowers is reduced by a ratio of 1·7.

Two further experiments under controlled temperatures made to determine the effect of day and night temperatures are worth describing.

In one experiment, plants of the varieties Potentate and Ailsa Craig were raised in glass incubators with natural indirect light. The seeds were sown on 15th April, 1947 and transplanted to the incubators on 25th April. The plants of each variety were divided into four lots of 24, one lot for each of four different temperature treatments; 25° C. day and night; 13°-16° C. day and night; 25° C. day (11 hours), 13°-16° C. night and 13°-16° C. day, 25° C. night.

Table IV gives the results; they show again the effect of low temperature and that plants, under alternating day and night temperatures, have flower numbers

TABLE IV.

Mean number of flowers in the first inflorescence under different day and night temperatures. (Natural illumination.)

Growing temp. (°C.)		Potentate	Ailsa Craig
Day	Night		
25°	25°	6·08±·38	8·43±·40
25°	12–16°	7·79±·39	8·42±·40
12–16°	25°	7·72±·38	9·00±·40
13–16°	13–16°	9·52±·40	9·35±·40

intermediate between the two extremes. Thus, under the conditions of natural illumination, the effect is the same whether the high or low temperature is in the light or dark period. The intermediate flower numbers merely express the intermediate number of hours given of either of the two temperatures.

A second test of a similar kind was made under the more accurately defined conditions of the controlled-environment rooms. The light period was 12 hours each day and the light intensity was 1,000 foot-candles. Under these special conditions the alternating day and night temperatures had a marked depressing effect on flower number as shown in Table V. This appears to conflict with the first test, and no satisfactory explanation can be offered. It is possible that the quality of the light may be a factor responsible for the difference.

TABLE V.

Mean number of flowers in the first inflorescence under constant temperature and alternating warm and cool conditions. Lighting by fluorescent tubes, 1,000 ft. candles at plant level and 12 hour day.

Growing temperature (°C.) Day	Night	Potentate
26°	26°	10·4±·65
26°	14°	6·4±·65
14°	26°	7·0±·65
14°	14°	13·7±·65

Finally the results of these experiments with four varieties under different conditions are brought together in Table VI. The bold figures are the temperature ratios derived from $\frac{N_1}{N_2}$ where N_1 is the number of flowers at the low temperature and N_2 the number at the high temperature. There are three conclusions to be drawn from Table VI.

1. Varieties differ in their response to temperature. Ailsa Craig with temperature ratios of 1·1 and 1·2 is a stable variety under widely different conditions. Kondine Red is more variable with a temperature ratio of 2·0 and is therefore only

TABLE VI.

Mean number of flowers in the first inflorescence (temperature ratios in bold type).

	Ailsa Craig	Potentate		Vetomold	Kondine Red
Cold frame	11·0			12·3	28·4
	1·2			**1·7**	**2·0**
Warm greenhouse	9·0			7·2	14·1
Controlled temperatures	Nat. Illum.	Nat. Illum.	Fluorescent tubes	F_2 Fluorescent tubes	
13°–16° C.	9·3	9·5	13·7	13·6	
	1·1	**1·5**	**1·2**	**1·7**	
25°–26° C.	8·4	6·1	10·4	7·8	

suited to rather specialized conditions. Potentate and Vetomold occupy intermediate positions.

2. The higher light intensity given by fluorescent tubes as compared with indirect daylight in April results in a higher number of flowers at both temperatures, cf. Potentate.

3. The temperature effect is smaller at higher light intensities than at low, cf. Potentate.

Duration of temperature effect—sensitive period.

Temperature treatments described in the previous section were given from a time when the cotyledons had just expanded to the first visible signs of the first inflorescence. This was 21 days at 24° C. and 42 days at 14° C. These long treatments were given to preclude the possibility of missing the sensitive period for the first inflorescence. After treatment, the seedlings were planted out in the open ground in Latin squares or randomized blocks. Thus any difference in mean flower number would be due solely to the temperature treatment given before the first inflorescence had fully developed. Any subsequent slight environmental effect

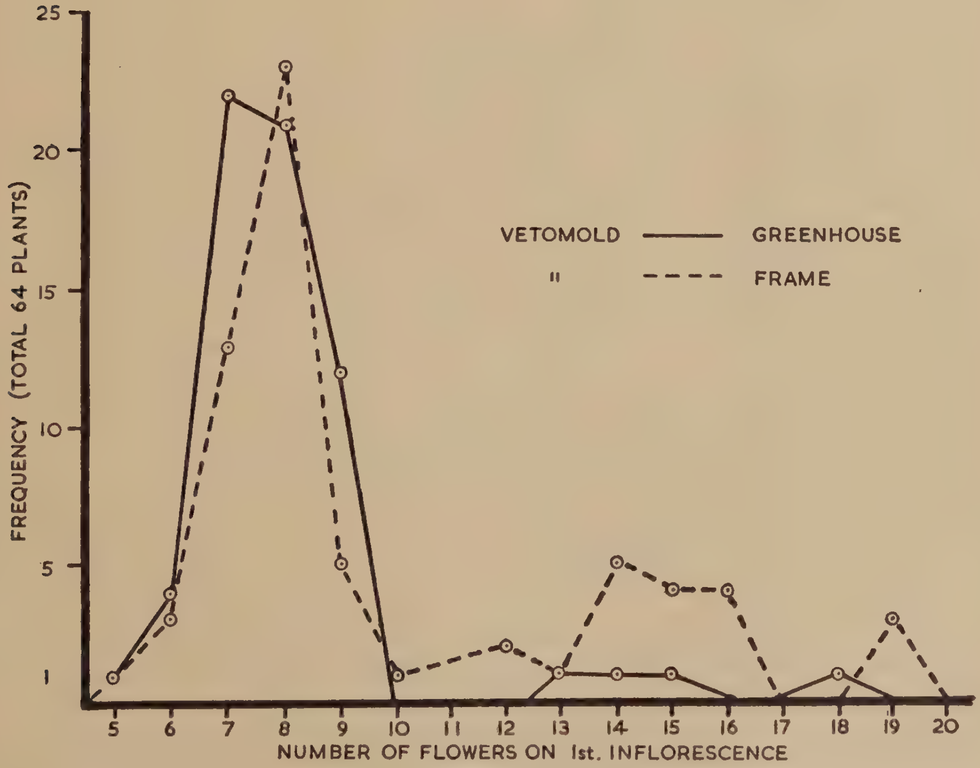

Fig. 1.

Distribution curves of inflorescences with different flower numbers showing bimodality due to single (first peak) and branched (second peak) inflorescences.

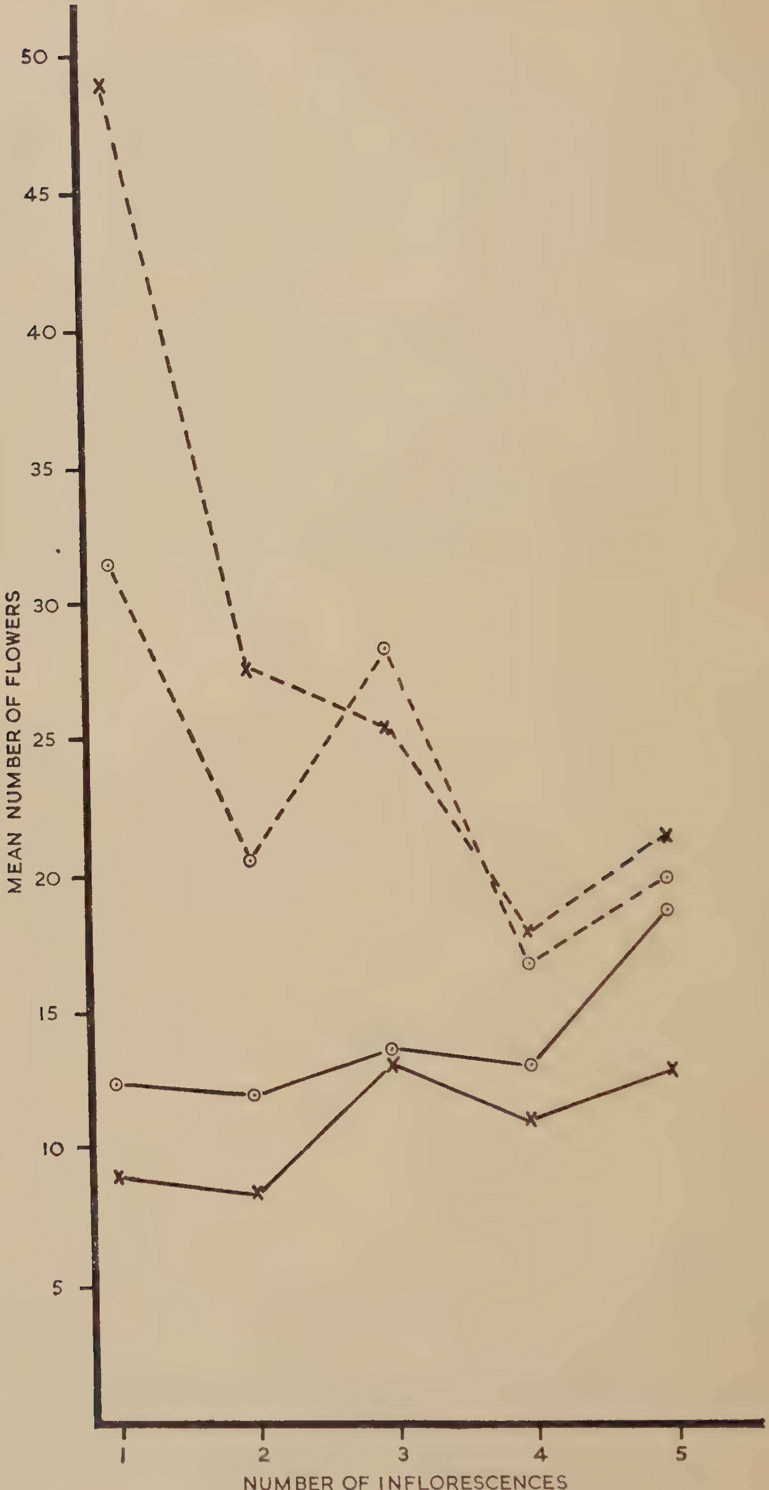

FIG. 2.

Effects of temperature on flower number in first five inflorescences; – – – low temperature; —— high temperature; **X**, F_4 selections (Kondine Red and Vetomold); ⊙, Kondine Red.

would be accounted for in the error variance of the analysis. Usually only the first inflorescence was counted, but counts on all the available inflorescences were made in 1949 on the varieties Kondine Red and Vetomold and, in 1951, on Kondine Red and an F_4 selection from a cross between the two varieties.

The results of the 1949 experiments were obtained from 256 plants in four 4×4 Latin squares planted at Merton. The differences in mean flower number between the varieties Kondine Red and Vetomold were highly significant for all four inflorescences. The differences due to temperature treatment of the seedlings were significant for the first two inflorescences in both varieties. The third inflorescence of Vetomold shows a difference of a size comparable to that in the first two, but it is not significant. Thus the effect of the early temperature treatment at Merton in 1949 lasted for the first two or three inflorescences.

The results obtained in 1951 with Kondine Red and an F_4 selection from an F_1 between Kondine Red and Vetomold are given in Fig. 2. There were 240 plants divided equally between varieties and temperatures and grown outside at Bayfordbury as part of three large randomized blocks.

The temperature treatments have produced large differences in mean flower number for the first three inflorescences in Kondine Red and the F_4 selection. The differences in the fourth and fifth inflorescence are smaller but still highly significant. Thus, in this year, the seedling treatment had a more lasting effect than in 1949. This is in spite of the fact that in both years the differential temperature treatments were given over precisely the same period of development.

It should be remembered that these temperature treatments, given as they were under natural light and without proper control in a warm greenhouse and cold frame, cannot be absolutely comparable except in the duration of treatments with regard to the stage of development.

The 1951 treatments gave a much bigger absolute difference as measured on the first inflorescence than did the 1949 treatments. This is evident from the figures given in Table III for Kondine Red and Vetomold. It seems probable that the larger immediate effect of the 1951 treatments is connected with the more lasting effect of that year. This points to there being two different actions of temperature on flower formation. Firstly there is the more direct effect of temperature on the early inflorescences which are actually laid down during the treatment. Secondly, there is a more indirect effect, brought about by the changed physiology of the plant, which may last to the fifth inflorescence, long after the temperature conditions have ceased to operate. It is significant in this connection that the F_4 selection and Kondine Red respond differently to the direct action on the first and possibly second inflorescence, but respond very similarly to the indirect action on the 3rd, 4th and 5th inflorescences (cf. Fig. 2).

An experiment to determine more precisely the duration of the sensitive period in development for the first inflorescence was carried out in the controlled temperature rooms. One room was kept at 26° C. and the other at 14° C. The light intensity at plant level was approximately 1,000 ft. candles and the light period was 12 hours. The plants were arranged in three randomized blocks in each room. The treatments consisted of dividing the time from cotyledon expansion to the appearance of the first inflorescence into periods and giving temperature treatments during these periods. The treatments and mean number of flowers are given in Figs. 3 and 4. Although the data in the two Figures are parts of the same test

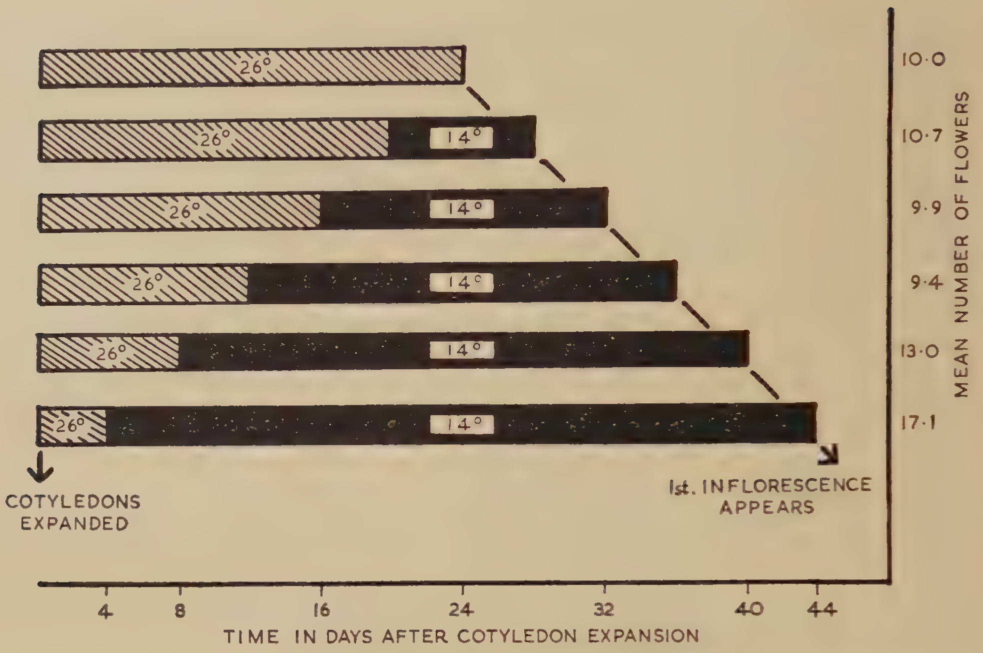

FIG. 3.

Diagram showing 6 different periods of high temperature treatment given to seedlings of Potentate. The number of flowers shown on the right indicates that the sensitive period is between 8 and 12 days. See text.

they are kept separate to clarify the description. The treatments represented in Fig. 3 started with the high temperature and the plants were then moved to the low temperature. The intervals of treatment were four days and the total length of time in the two temperatures was constant for all treatments if we assume that for developmental purposes the time at 26° C. has twice the value of the time at 14° C.; or $T_{26}=2T_{14}$. The mean number of flowers in the first inflorescence shows a consistent and decisive effect of the different treatments. Thus treatments in which the first 12 days or more are at the high temperature are all alike in producing a low number of flowers (10·0).

High temperature extending to the 8th day, and thereafter a low temperature, produces a larger inflorescence (13·0). This is the same size as that resulting from continuous low temperature treatment, cf. Fig. 4. These clear cut results indicate that the sensitive period is between the 8th and the 12th day after cotyledon expansion.

The number of flowers produced by a high temperature up to the 4th day is the highest of all treatments. The fact that it is higher than the continuous low temperature shows that the alternation of hot and cold periods at this early stage of growth introduces yet another effect on flower production.

The converse treatments, that is, starting the plants in the cold and transferring them to the warm are given in Fig. 4. For the main object of the experiment these results are highly unsatisfactory. Firstly, there is an unexpected effect of a prolonged low temperature period followed by a short period of high temperature having

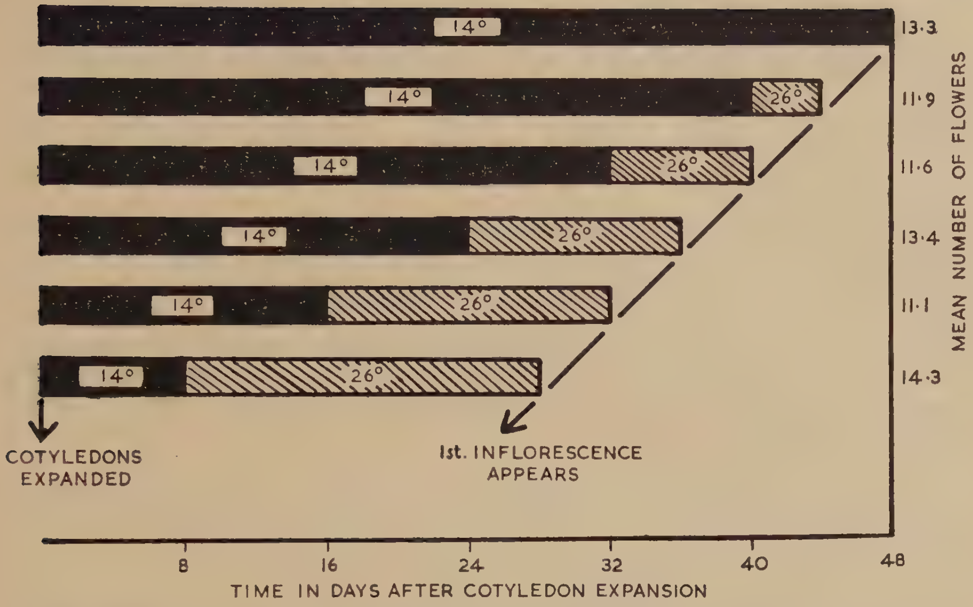

Fig. 4.

The six different periods of low temperature are the converse of the treatments shown in Fig. 3. There appears to be no simple temperature effect. See text.

a significant lowering effect on flower production. Secondly, there is the unaccountable variation around the 24-day cold treatment. It would appear that transferring plants from the cold to the warm alters the physiology of the plant and thus has an indirect effect on flower production. Only further experiments would disentangle these effects. But the high number (14·3) obtained with the low temperature for the first 8 days does agree with the conclusion from the results of the converse treatments, which were quite unambiguous.

Practical application.

The number of flowers of the fourteen varieties given in the appendix are from plants which have been raised under good commercial conditions. These plants were raised for outdoor planting, i.e. they were sown about 15th April. If the number of flowers in the first inflorescence of Kondine Red, Ailsa Craig, Potentate and Vetomold are compared with the figures obtained for these varieties under controlled temperatures it will be seen that commercial practice produces a plant which has a low number of flowers. In other words in commercial practice the temperature during early plant growth is too high for the low light intensity and short days which prevail during the early months of the year.

That this difference in the first inflorescence between the " controlled " and " commercial " plants is due to the conditions of raising the plants is shown by the fact that there is good agreement in flower number if the later inflorescences are compared. The conditions prevailing at the times when these later inflorescences were laid down would be comparable in the two lots of plants.

Of greater importance are the conditions for raising plants used for greenhouse crops. These have smaller inflorescences than have plants raised for outdoor planting (Mather, 1948). This is probably due to the earlier sowing and in consequence to lower light intensities and shorter days. It is at this time of the year that the temperature effects on flower production are most pronounced and when every effort should be made to keep the temperature down as low as practicable for healthy growth.

The practical importance of the temperature and light effects on inflorescence size will depend upon the variety. Varieties like Ailsa Craig which have a small temperature ratio are little affected. But for varieties like Potentate and Vetomold, with large temperature ratios, these factors are of considerable importance. Since the weight of the early crop will not only depend upon the earliness of ripening, as measured by the date of the first fruit, but also on the number of flowers in the first inflorescence, it is important for such varieties to have the right conditions for maximum flower production.

In producing an early crop there are two opposing effects ; high temperature accelerates growth but lowers flower production. To obtain plants with high flower production and flowering as early as the plants grown under commercial conditions, they must be sown earlier and grown under cool conditions.

Earlier sowing has its disadvantages, and, from this aspect of the practical problem, the temperature-sensitive period is of importance. This period has been broadly defined for the first inflorescence as the 8-12 day period after cotyledon expansion. If a low temperature is maintained only for this period then high flower production would be obtained with a minimum retardation of growth.

SUMMARY.

1. There are three main factors affecting the size of the inflorescence in tomatoes. (1) A major gene. (2) A system of polygenes which is largely responsible for the differences in mean number of flowers in cultivated varieties. (3) The environment.

2. The branching of the inflorescence is a variable character which is bound up physiologically with the number of flowers. But branching, whether it is due to environmental factors or variety, is the result and not the cause of increased flower production.

3. Temperature and light are the most important environmental factors affecting inflorescence size. A low temperature (14° C.) during the growing period, from the expansion of the cotyledons to the appearance of the first inflorescence, causes an increase in flower production as compared with plants raised at 25°-30° C. In the variety Kondine Red the increase is twofold.

4. Plants grown entirely under artificial light show a similar temperature effect to that shown by plants growing in natural light. High light intensity and/or day length increases flower production.

5. Alternation of warm days and cool nights and *vice versa*, as opposed to a uniform temperature, had no effect on flower number in plants grown under natural light, but both had a depressing effect on flower production under artificial light.

6. The sensitive period for the temperature effect on the first inflorescence is between the 8th and 12th day after cotyledon expansion. Treatments given from the time of cotyledon expansion to the emergence of the first inflorescence have an effect which sometimes lasts to the fifth inflorescence.

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APPENDIX.

FLOWER NUMBER IN TOMATO VARIETIES.

By M. B. CRANE and A. G. BROWN.

The records of the number of flowers on the first to the fifth inflorescences given in the following table were made during experiments carried out to determine the time of maturity and yield of varieties of tomatoes. The tomatoes were grown out of doors during the years 1941 and 1942 and the work was an essential preliminary to an investigation concerning the possible utilization of hybrid vigour in tomatoes.

Tomato varieties. Number of flowers per inflorescence (Mean of 1941, 1942).

Variety	Inflorescence					Mean
	1	2	3	4	5	
Kondine Red	13·0	19·6	20·6	15·8	14·0	16·6
Market King	12·3	16·4	12·7	16·9	20·7	15·8
Radio	10·3	15·4	15·3	17·1	17·0	15·0
Harbinger	12·2	16·3	17·8	15·3	12·0	14·7
Ailsa Craig	10·0	14·1	13·8	12·8	16·3	13·4
Leafmould Resister No. 1	11·9	10·3	11·6	13·1	13·8	12·1
Stonor's Progress	11·7	12·9	11·1	12·5	10·9	11·8
Plumpton King	10·0	11·1	11·7	12·1	13·0	11·6
Sunrise	9·9	10·8	11·6	12·1	12·8	11·4
Stonor's Exhibition	11·3	11·2	11·6	11·8	10·7	11·3
Potentate	10·5	11·0	11·5	10·4	10·0	10·7
Moneymaker	10·7	8·3	10·0	10·7	11·1	10·2
Earliest of All	9·5	10·2	7·8	10·6	11·7	9·9
Vetomold	6·6	8·5	9·7	8·0	9·2	8·4

The number of flowers per inflorescence is the average from sixteen plants. The results show that there are considerable differences between varieties in the number of flowers produced. Differences also occurred in the different years, but those that gave the greater number in 1941 usually gave the greater number in 1942.

In 1941 the highest number of flowers occurred most frequently on the fourth inflorescence, whereas in 1942 most varieties had the highest number on the fifth inflorescence. In 1942 conditions were poor for tomatoes growing out of doors ; fruit setting and yield were much lower in that year than in 1941 and this, resulting in a smaller amount of fruit developing in 1942, undoubtedly accounted for the high flower number on the fifth inflorescence.

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REVIEWS

THE MOLECULAR ARCHITECTURE OF PLANT CELL WALLS. By R. D. PRESTON. (London: Chapman & Hall. 1952. Pp. 211, illus. Price 36s.)

Botanists and others interested in plant science are aware that during the last thirty years or so certain physicists have been making a close examination of natural cellulose, using such powerful tools as the X-ray spectroscope and the electron microscope. It has leaked out that something new and fundamental is coming to light concerning plant cell walls, something that the botanist feels he ought to know, but to him the necessarily highly technical jargon of unfamiliar techniques, in which the original papers are couched, presents such a barrier that often he finds it difficult even to grasp exactly what discoveries are claimed; much less can he examine the evidence and foresee the implications. In this book, Dr. R. D. Preston undertakes to act as guide to those who seek a path across the barrier and rewards those who walk with him, not merely with a glimpse, but with a conducted tour of the Promised Land, so far as it has as yet been revealed.

To those whose training has mainly been in other branches of science, the path to be followed is arduous, but Dr. Preston rightly feels that he would be doing botanists and others a poor service if he presented the results of research in a series of *ex cathedra* statements. He, therefore, devotes nearly half his book to an exposition of the underlying principles on which the physical methods are based. Without some understanding of these principles, neither appreciation of the elegance of both experimentation and logical deduction nor critical appraisal of the results is possible.

The book begins with two excellent introductory chapters, while a third gives an outline of the chemical nature of cell-wall constituents. There follows an attempt to present the fundamental bases of the methods of analysis of structure by optical and X-ray methods. To the reviewer it seems doubtful if the difficulty of the subject to the reader, presumed to have at most but a moderate knowledge of modern physics, has here been sufficiently appreciated. Greater clarity could only be obtained, perhaps, by expansion of this section, but it would be a justifiable expansion. Much that is to follow, for example, is based on the interpretation of "rotation photographs", but it is feared that neither the text nor the diagram purporting to explain the essentials will make the tyro much wiser. The succeeding chapter, after dealing with the molecular weight of cellulose and the Micellar Hypothesis, goes on to describe the production of electron micrographs—an excellent example of which provides an appropriate frontispiece—so concluding the first section of the book.

The second and larger section is concerned with the consideration of wall organization in plant cells in terms of the submicroscopic structure of cellulose. Step by step it is shown how the nature of what might loosely be described as a "ply-wood" structure has been deduced for various cell-walls, ranging from the "three-ply" conifer tracheids to the "multi-ply" walls of *Valonia*. Discussion of wall structure in these thick cell-walls turns attention to the primary walls of growing cells and ineluctably we are led in the grand finale to a consideration of the mechanism of orientation and growth.

It is a fascinating story, delightfully told, one requiring close attention, maybe, but rewarding, for the author not only gives the facts, so far as they are known, but also attempts to show them in their true setting as a record of cellular activity throwing light on the most fundamental processes of growth. Here our guide becomes philosopher and friend as well. As a philosopher, he follows a logical path to the frontiers of knowledge to peep at what may lie beyond. As a friend he is eager to share the pleasure and excitement he has found as one of the leaders in the difficult and laborious work of exploration. In all three capacities he is strongly recommended. Dr. Preston himself is to be congratulated on the production of an outstanding book.

A.E.B.

LA VIE DES FRUITS. By R. ULRICH. (Paris : Masson et Cie. 1952. Pp. 370, illus. Price 2,000 fr.)

During the last 50 years a vast mass of information has been obtained on the structure, physiological processes and composition of fruits. In *La Vie des Fruits* an attempt is made to bring together and integrate this scattered information in the space of one volume. It is an ambitious undertaking, but M. Ulrich, Director of the Biological Laboratory of the Station du Froid (C.N.R.S.) is to be congratulated on the masterly and discerning way in which he has handled his material. As he states in the preface, this is not a monograph on the edible fruits, species by species. It is rather an exposition of the life processes of a fruit, the general principles being amplified by reference to the behaviour of particular fruits.

The field is systematically covered. A brief introduction on the structure of the flower is followed by an analysis of the factors leading to fruit set or parthenocarpic development. Then comes a classification of the main stages in the life of a fruit, the morphological and cytological changes that take place during growth and the conditions affecting growth. The next two sections deal with the form and structure and with the composition of ripe fruits. Following on from this is a detailed technical account of the various gaseous exchange processes, a subject on which the author has done much research, and the transformation of chemical substances within a fruit during development. Finally, come three short sections which contain much of practical interest to the grower ; one on maturation and maturity dealing with maturity tests, factors affecting ripening and disorders of ripening, one on senescence, dehiscence and fruit fall, including control of fruit fall by growth substances, and one by M. Viennot Bourgin, Professor at the Institut Agronomique, on fungous diseases.

Although the scope of the book is so wide, the treatment is rarely superficial. By covering the processes of development step by step and defining each technical term as it arises, the author has managed to deal even with complex biochemical reactions in a way that is comprehensible to the non-specialist. Much of the general information is supplemented by detailed experimental results and graphs but, where the limitations of space have made this impossible, as notably in the chapter on factors affecting growth, the student can be guided by the admirable bibliography. Although this does not claim to be comprehensive, it contains over 1,000 references and is arranged according to the subject matter of the various chapters. Indeed, it is probably as a collation of the literature that this book will be of most value to the research worker. The line drawings, largely taken from other sources, are well chosen and helpful.

P.R-D.

THE INJURIOUS INSECTS OF THE BRITISH COMMONWEALTH (EXCEPT THE BRITISH ISLES, INDIA AND PAKISTAN) WITH A SECTION ON THE CONTROL OF WEEDS BY INSECTS. By J. W. Evans. (London : Commonwealth Institute of Entomology. 1952. Pp. 242, illus. Price 30s.)

The volume is arranged in five parts. The first part gives a short review of the environmental conditions and chief crops of each country, followed by titles of comprehensive publications, and reference is made to the more important insect pests of crops. The insects of medical and veterinary importance are dealt with briefly. The second part relates to insect and crop associations, and the third with the insects of horticulture, forestry and agriculture. In this section the insects are arranged alphabetically under families and genera within the main orders of classification. Part four concerns weed control by insects, and brings together in a readable manner the scattered literature on the subject, and outlines the attempts that have been made to control harmful weeds by means of insects. Records are included of the indigenous insects which feed on noxious plants. Part five is more general and relates to such important problems as plant quarantine, virus vectors, insect control and research needs.

A feature of this valuable work is the novel method by which references are quoted, a method which dispenses with a detailed bibliography. As stated in the Introduction, the greater part of the information has been obtained from the volumes of the *Review of Applied Entomology*, and reference is made merely by citing volume and page.

This work will provide references for information on the injurious insects of the Commonwealth, and will prove indispensable to all those engaged in the field of Applied Entomology.

The book opens with a frontispiece of Sir Guy Marshall, K.C.M.G., D.Sc., F.R.S., who was the Director of the Imperial Institute of Entomology from 1913-1942, and it is indeed a fine tribute to the one man who has done so much to foster the study of economic entomology in the Commonwealth countries.

A.M.M.

METHODENBUCH BD. 8, "DER VEGETATIONSVERSUCH", 1. "DIE METHODIK DER WASSERKULTUR HOEHERER PFLANZEN". By W. Schropp. (Neumann Verlag, Radebeul und Berlin. 1951. Pp. 309, illustrated. Price 22 DM.)

This is a survey of 40 years' work on elaborating and applying hydrocultural methods. After discussing physiological fundamentals the author describes various technical methods and presents devices for controlling growth factors during vegetation. He gives a thorough survey of a great number of complete and deficiency nutrient solutions. The effects of nutrient factors upon growth and behaviour, especially deficiency appearances, can advantageously be tested by hydroponic methods and this is clearly demonstrated by more than a hundred good photographic pictures. Special reference is made to the economical side of hydroponics on a commercial basis.

The book being the first complete one of its kind will be valuable for individuals and institutions concerned with scientific and commercial plant growing.

W.G.
G.L.

THE DIAGNOSIS OF MINERAL DEFICIENCIES IN PLANTS BY VISUAL SYMPTOMS. By T. WALLACE. (London: H.M.S.O. 1951. Second edition. Pp. 107, illus. Price 35s.)

The second edition follows the same lines as the first but with a few additions to the letterpress, such as brief mention of molybdenum which has become of greater interest since the first edition.

A whole-page table is devoted to " healthy and deficiency values of mineral elements in various crops ". An appendix has been added to Chapter III on "Details of technique for chemical tissue tests ". This occupies eight pages. There are 312 coloured plates, compared with 114 in the original edition, and 209 in the Supplement to that edition. Their quality is much improved. They are arranged according to plants, instead of according to deficiency, as in the original edition and Supplement. This is a big improvement from the point of view of one using the book in the field.

W.A.R.

MANUAL OF BACTERIAL PLANT PATHOGENS. By CHARLOTTE ELLIOTT. (London: Wm. Dawson & Sons, Ltd.; Waltham, Mass: The Chronica Botanica Co. 1951. Second edition entirely revised. Pp. 186, illus. Price $6.)

Since the recognition of the bacteria as important plant pathogens, towards the end of the last century, an extensive literature has accumulated on these organisms and the diseases they cause. In 1930, in her *Manual of Bacterial Plant Pathogens*, Charlotte Elliott collected all the exisiting literature and in so doing provided plant pathologists with the first comprehensive compendium of the plant pathogenic bacteria.

The last twenty years have seen a rapid expansion of our knowledge of these organisms, particularly in the field of nomenclature and classification. As a result of these advances, the need for a revision of the *Manual of Bacterial Plant Pathogens* has been apparent for some time and the publication of this second edition will be welcomed by all microbiologists.

The presentation of material is along the same lines as in the original edition. In Part I the bacteria are listed in alphabetical order together with their synonyms, chief morphological and cultural characteristics, a description of the disease symptoms they cause, and a summary of the chief control measures. Under each species an extensive chronological list of references is given. Part II is a list of some hundred odd organisms associated with plant diseases but not recognized as valid pathogens. The chronological chart of plant pathogens (Part III of the original edition) has this time been wisely excluded. Two indexes are provided, one for the bacteria and one for the host plants. The latter will prove invaluable to those anxious to know the pathogens already associated with a particular host. The bacteria are indexed by their specific epithets; this makes for easier reference and it will not be so readily invalidated by any further revision of generic nomenclature.

Apart from the incorporation of much new material, including references and descriptions of several new species described since 1930, the major difference between the old and new editions is in the nomenclatural system adopted. This follows current American ideas on the subject, with gram negative genera *Pseudomonas* and *Xanthomonas* for the lophotrichous forms, and *Erwinia* and *Agrobacterium* for the peritrichous bacteria. The gram positive pathogens are included in the genus *Corynebacterium*.

The only serious criticism of this book concerns the bibliography. When an exhaustive list of references of this kind is given, it is a great advantage if important ones can be readily distinguished from those containing a small note or comment on a disease, especially in these days, when it is difficult enough to keep abreast of current literature. Unfortunately this is not the case here, the only indication to the content of a paper being its title, which often is not very illuminating. Amplification of selected references by short notes or abstractions would have considerably increased the usefulness of the book, even if this had been done to the exclusion of the lists of cultural characteristics given under each pathogen. It is difficult to see what purpose these cultural lists serve. They add little to those already given in Bergey's *Manual* and are frequently incomplete, although, except in a few cases, e.g. *Pseudomonas mors-prunorum* (wrongly described as gram positive), this is no fault of the author's. For some genera there is obviously a need for a relatively clear and simple system of identification, but in the present state of our knowledge it is doubtful whether this is yet possible. In the meantime, anyone seriously interested in the characteristics of specific organisms would be best advised to refer to original papers on the subject.

The author must be congratulated on the obvious care devoted to the production of this new edition, which despite these criticisms remains an invaluable contribution to phytopathological literature.

J.E.C.

SANDERS' ENCYCLOPAEDIA OF GARDENING. Revised by A. G. L. HELLYER. (London: Collingridge. 1952. Pp. 524. 23rd edit. Price 21s.)

Sanders' Encyclopaedia of Gardening was first published in book form in 1895, following a lengthy parturition of five years in the columns of *Amateur Gardening*, since when the horticultural community have never been without it. Its record of 23 editions (28 impressions) is sufficient testimony to the esteem in which it is held. Since its first appearance there has, of course, been an ever-flowing stream of new introductions, and also many changes of nomenclature brought about by the now accepted rule of priority.

In the new edition great pains have been taken to incorporate this new material and to bring the book fully up to date. To many the dubbing of old favourites with new, and somehow always less euphonious, names is an exasperation engendering hard thoughts of " pedants ". The Editor recognizes this and, if not quite in words of one syllable, at least with great simplicity and clarity, he explains in a foreword the reasons for the changes and, in fact, the whole system by which plants are named. The reader should now at least be convinced that the changes are not made just for fun.

Those unfamiliar with the book might suppose from the title that the entire range of gardening operations is included. This is not so. The book might be described as an *Index Kewensis* in miniature, though with considerably more descriptive matter than those august tomes are accustomed to provide. The aim is to list every species (not horticultural variety) in cultivation if of garden value, the English name, where there is one, details of height, colour, habitat and time of flowering, the general cultural requirements of the genus and the special needs of any exacting species. Also, John Innes standard composts notwithstanding, the soil mixtures traditionally assigned to various kinds of pot plants are included. These recipes, for number and complexity, leave Mrs. Beeton well down the course but to have eliminated them would have been to deprive many gardeners of one of their chief pleasures. All this information is presented in compact almost telegraphic form without a superfluous word. The book, though no longer one for the pocket, is certainly one for the shelf.

G.St.C.F.

THE HEATHER GARDEN. By Fred J. Chapple. (London: W. H. & L. Collingridge Ltd. 1952. Pp. 180, illus. Price 21s.)

The author has grown heathers and heaths for over 25 years, and considers that they provide the ideal labour-saving garden plants. The details he gives of heather culture go far to show that this is so. Nearly three hundred species and varieties of *Calluna* (heather or ling), *Erica* (heath) and *Daboecia* (Irish heath) are described; and a " heather calendar " shows which ones are in flower in each month of the year. In a chapter on soil, the author maintains that almost any soil that is not too rich or impregnated with lime is suitable for heather culture. Other chapters deal with propagation, schemes for the heather garden, and shrubs and trees suitable for growing with heather.

There are over 50 attractive illustrations, but the fact that reference is hardly made to them in the letterpress lessens their value. This is not a scientific treatise but will form a useful addition to the bookshelf of any scientific gardener.

W.S.R.

SAND AND WATER CULTURE METHODS USED IN THE STUDY OF PLANT NUTRITION. By E. J. Hewitt. Technical Communication No. 22 of the Commonwealth Bureau of Horticulture and Plantation Crops. (Commonwealth Agricultural Bureaux: Farnham Royal, Bucks. 1952. Pp. 241, illus. Price 42s.)

There has for long been need for a critical compilation of all the available data on methods for the research study of plant nutrition. In this work Dr. Hewitt of Long Ashton has undertaken the enormous task of reviewing all the literature and condensing it into a single volume, which must become the standard reference book for investigations in the field. The magnitude and scope of the work is indicated by the fact that thirty pages, covering some eleven hundred citations, are occupied by the bibliography and, so far as tests reveal, all these papers are referred to in the text. This bibliography alone, covering not only papers on nutrition but every aspect of environmental control, will prove of the greatest importance to research workers and will save them endless searching of the literature.

The book is divided into two parts; the first constitutes the general review of all published data on techniques related, however distantly, to sand and water cultures. A detailed and critical analysis of every aspect of these methods is provided; the shape, size, composition and preparation of containers, the mechanical and chemical analyses and the purification of rooting media, the sources, character and purification of water, the composition, reaction and methods of application of the nutrient solution, these are only some of the main subjects considered. No point is too small to escape the author's notice and critical consideration. The review is extended to embrace techniques for the control of all other factors of the environment besides the nutritional and includes also the field of aseptic culture of embryos and seedlings.

The second part of the book deals with the special technique developed at Long Ashton, mainly by the author himself, for large-scale pot sand culture and shows how efficiently a system has been evolved which takes account of all the points reviewed in the earlier part and which has made possible the great advances in our knowledge of nutritional problems in general and of the roles of the micronutrients in particular, which we owe to the team under Professor Wallace's direction.

Dr. Hewitt and the Commonwealth Bureau of Horticulture and Plantation Crops have done a real service to research workers in the production of this volume.

R.H.S.

STOCK AND SCION INVESTIGATIONS

IX. TWELVE YEARS OF ROOTSTOCK EFFECT IN AN APPLE ORCHARD TRIAL

By L. A. THOMAS*

Commonwealth Scientific and Industrial Research Organization,
Division of Plant Industry

This paper presents a record of the growth and cropping of Jonathan and Granny Smith apple trees on seedling and clonal rootstocks at twelve years after transplanting the trees from the nursery. Details concerning the origin of the investigation are presented in an earlier paper (Dickson and Thomas, 1938), where this part of the rootstock studies at Stanthorpe is referred to as the Main Trial.

MATERIAL AND METHODS.

The Malling stocks M.I, II, XII and XVI used in the trial were obtained from the East Malling Research Station and propagated at Stanthorpe. The root-grafted Granny Smith trees on M.XIII were supplied by the New South Wales Department of Agriculture. Northern Spy rootstocks, Pomme de Neige seedlings and Jonathan trees on French Crab seedlings were obtained from selected nurserymen. The so-called French Crab seedlings were simply seedlings imported from France and are not to be confused with seedlings from the apple variety, "French Crab".

Fifty of each of the stocks required were stem-budded to Jonathan and Granny Smith and thirty trees of an even grade were selected from the trees produced. As woolly aphids infested the roots of some trees on the Malling and seedling rootstocks, all trees except those on Northern Spy were thoroughly dipped in a nicotine sulphate and soft soap bath before transplanting.

Layout of the trial.

The trial was planted in six randomized blocks ; within each block were five plots each containing five Jonathan trees on the following rootstocks : Malling I, XII, XVI, Northern Spy and Pomme de Neige seedlings ; and five plots of Granny Smith trees each containing four trees on M.XII and M.XVI, Spy and Pomme de Neige seedlings. The trees in each plot were randomized. The internal guard trees consisted of thirty trees each of Jonathan on French Crab seedlings, Granny Smith on M.II and on M.XIII rootgrafts. External guard trees were Jonathan on M.II and Granny Smith on M.XIII rootgrafts. The trees were planted in 1938 at twenty feet apart on the square system ; all trees were two years old at planting, with the exception of Jonathan on French Crab seedling stock and Granny Smith rootgrafts on M.XIII, which were yearlings.

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* An officer of the Division of Plant Industry located at Stanthorpe, Queensland.

Fertilizer treatments.

The five Jonathan plots in each of the six blocks were used to test the effects of five fertilizer mixtures which were composed of sulphate of ammonia, superphosphate and muriate of potash. The composition of these mixtures is given below as pounds per tree of each ingredient in the order N, P, K.

Mixture 1	2 : 2 : 1
2	4 : 2 : 1
3	2 : 2 : 1 plus 2 : 0 : 0
4	2 : 2 : 2
5	2 : 0 : 2

All mixtures were applied in spring approximately two weeks before blossoming, except the extra 2 lb. of sulphate of ammonia in Treatment 3, which was applied after fruit set. From 1939 until 1948, the rate of application was that indicated by the composition of the mixture in pounds weight ; in the 1949 season the rate was increased by half. Each Jonathan plot had the appropriate amount of fertilizer spread over the 20 ft. squares on both sides of the trees ; thus the trees in the alternating Granny Smith plots were treated as guard trees for the purpose of testing the effect of fertilizers on the Jonathan trees. As the fertilizer treatments for the Jonathan plots were randomized in each block, the trees in the Granny Smith plots thus received a different fertilizer mixture on either side.

Pruning.

All trees were winter pruned to an open-centred vase-shaped tree. Two thirds of the annual leader growth on the Jonathan trees was pruned away and three quarters of the length on the Granny Smith trees. Laterals on Jonathan trees were pruned to five buds and fruiting wood was kept close to the leaders. With Granny Smith, the lateral growths were pruned back to form spur systems. Sub-leaders were developed wherever there was room for extra growth to be placed in the framework of the tree.

Thinning of the fruits set.

As a general guide to thinning, all fruit set was removed from the previous season's wood on the leaders ; all other clusters were reduced to two fruits. Although in some seasons the trees carried very heavy crops, any extra thinning was confined to spacing fruits to prevent their being pushed off the tree before maturity. This extra thinning was necessary for Jonathan trees only, as the Granny Smith trees did not set such heavy crops.

Green manure crops.

In the autumn of each year the trial received a dressing of 1¼ cwt. per acre of a fertilizer mixture, made up of three parts of superphosphate and one part of sulphate of ammonia, prior to sowing a green manure crop. Golden tares were first used, then New Zealand Blue Lupins and latterly Black Winter Rye.

Minor element deficiencies.

As a safeguard against the effects of known minor element deficiencies, copper was supplied as a copper sulphate soil dressing at the rate of one-half pound per tree in 1939, the year after planting, when copper deficiency symptoms were already in evidence. Zinc sulphate sprays were applied every alternate winter from 1940 until 1946 to counteract a possible zinc deficiency, and thereafter as a summer spray at the rate of three pounds per hundred gallons of spray mixture. When boron deficiency symptoms were recognized (Thomas, 1944), borax was applied in summer sprays at the rate of 5 lb. per 100 gallons of spray mixture. Dolomite at the rate of 1 ton per acre was applied in 1947.

Records.

Records made included total annual shoot growth from 1938 until 1941, girth of trunk at a fixed height above the union, height and spread of trees at intervals, number and weight of fruit annually.

RESULTS.

Annual shoot growth.

The accumulated growth per tree over the first four seasons on five rootstocks is presented in Table I, where it will be seen that, at this stage of growth, the vigorous habit of trees on M.XII had become evident.

TABLE I.

Accumulated growth in metres per tree, 1938-41.

		a. Jonathan		
M.XII	M.XVI	Seedlings	M.I	Spy
132·0	86·8	77·4	77·4	68·4
		b. Granny Smith		
93·7	75·7	61·2	—	64·0

Minimum difference for significance at 1 per cent.

for Jonathan	15·7
for Granny Smith	13·0

Girth of trunk.

The data for girth measurements of Granny Smith trees in the even-numbered years are presented in Table II. Trees on M.II and M.XIII in the internal guard rows may be considered comparable and are included for comparison.

TABLE II.

Granny Smith—trunk girth in cm.

Stock	1938	1940	1942	1944	1946	1948	1950
M.XII	7·7	14·4	23·2	31·3	37·6	42·2	46·9
M.II	5·9	13·6	22·9	30·4	35·1	38·4	42·6
M.XVI	7·5	14·1	22·7	29·4	34·2	37·9	41·4
Seedlings	7·1	12·9	20·7	27·0	31·1	34·9	38·4
Spy	6·8	13·5	21·5	27·7	30·6	33·0	36·3
M.XIII	3·8	9·5	16·8	22·8	26·5	28·9	31·7

An analysis of the logarithms of the 1948 girth measurements yielded the following statistical data.

Stock	Mean log girth	Geometric mean girth (cm.)
M.XII	1·623	42·01
M.II	1·582	38·18
M.XVI	1·578	37·82
Seedlings	1·532	34·03
Spy	1·516	32·84
M.XIII	1·458	28·69

Minimum difference between log girths of trees on M.XII, M.II, M.XVI, Spy and M.XIII
significant at 5%—0·021
1%—0·028
0·1%—0·036
Minimum difference for comparison of seedling stocks with the rest
at 5%—0·040
1%—0·053
0·1%—0·069

The girth measurements of the Jonathan trees are given in Table III where the measurements for the even-numbered years are tabulated. For purposes of comparison, the figures for trees on French Crab seedlings and on M.II are included in the Table, but not in the statistical analysis.

TABLE III.

Jonathan—Girth of trunk in cm.

Rootstock	1938	1940	1942	1944	1946	1948	1950
M.XII	7·5	14·8	25·4	35·3	40·8	44·0	48·6
M.XVI	7·1	13·2	21·5	29·7	34·9	38·7	42·8
Seedlings	6·8	12·9	21·2	29·4	34·1	37·7	41·8
Spy	6·2	11·8	18·8	24·6	27·4	29·7	33·2
M.I	6·4	12·5	20·5	26·9	28·8	30·0	32·0
French Crab Seedlings ..	3·2	9·9	18·7	27·8	34·8	39·5	44·4
M.II	6·1	12·1	20·0	27·6	31·3	35·0	40·1

The statistical data are presented below, using the 1948 circumference measurements.

Rootstock	Mean log girth	Geometric mean girth (cm.)
M.XII	1·646	44·3
M.XVI	1·586	38·5
Seedlings	1·568	37·0
M.I	1·481	30·3
Spy	1·472	29·6

Minimum difference between mean log girths significant at 5%—0·030
1%—0·039
0·1%—0·051

From the data it will be seen that, with the four rootstocks common to both scions, the same relative order of growth is shown; the trees decrease in girth in the order M.XII > M.XVI > Seedlings > Spy.

The semi-dwarfing stock M.II, which Hatton (1928) classed with Spy, has with both scions produced much stouter trunks.

The Jonathan trees on French Crab seedlings, although one year younger than those on Pomme de Neige seedlings, have a greater average girth of trunk.

Variation in tree size.

It is a widespread belief among orchardists that trees on seedling stocks are not only vigorous but are of a uniform size. That trees on seedling stocks can be more variable in size than those on vegetatively reproduced stocks is demonstrated in this experiment. Using the girth measurements above, the following coefficients of variability (V) are submitted for comparison.

Jonathan on M.XII	9·1
Jonathan on Pomme de Neige seedlings	15·8
Granny Smith on M.XII	9·1
Granny Smith on Pomme de Neige seedlings	20·8

With these, Jonathan on French Crab seedlings, V = 15·2, can also be compared.

Height and spread of tree.

These measurements are of limited usefulness to describe the growth habit of trees as they are altered by the bearing of crops, when leaders are usually bent outwards and downwards. When there is a wide range in tree size produced by a series of rootstocks, or when the shape of a scion variety is modified by a particular rootstock, then these measurements are of value. The height and spread of the trees, as measured in 1948, are presented in Table IV.

It will be seen that the order for size of tree, as given by the product height × spread, is approximately the same as that of the girths. The difference in the height of the Jonathan and Granny Smith trees on similar stocks is not great, with the exception that the Granny Smith trees on Spy stocks are taller than the Jonathan trees. Jonathan trees are more spreading than Granny Smith, particularly on the more vigorous stocks M.XII, M.XVI and Seedlings.

TABLE IV.

Average height and spread in feet, 1948.

Rootstock :—	M.I	M.XIII	Spy	Seedlings	M.XVI	M.XII	French Crab seedlings	M.II
	a. Jonathan trees							
Height	8·3		9·0	9·7	10·5	11·6	10·0	8·6
Spread	6·6		7·8	8·3	8·6	8·9	8·0	7·9
Height × Spread	54·8		70·2	80·5	90·3	103·2	80·0	67·9
	b. Granny Smith							
Height		8·2	9·9	9·5	10·7	11·6		9·4
Spread		5·7	6·9	6·7	7·6	7·6		7·7
Height × Spread		46·7	68·3	63·7	81·3	88·2		72·4

Cropping

The annual crops of fruit from each tree were counted and weighed. The cropping record for Jonathan is presented in Table V. There are no crop records for 1949, as a late frost on 23rd October totally destroyed the young fruits.

TABLE V.

Jonathan. Average crop per tree (*lb.*).

Rootstock	1943	1944	1945	1946	1947	1948	1950	Total
M.XII	1·6	23·4	20·2	81·1	134·8	208·7	264·7	734·5
M.XVI	2·0	30·7	21·2	74·9	124·9	140·6	230·3	624·6
Spy	3·9	36·3	30·8	108·2	89·4	149·5	155·1	573·2
Pomme de Neige seedlings	2·3	26·0	24·4	73·4	112·5	122·3	171·3	532·2
M.I	5·6	39·4	45·7	90·6	69·6	109·0	125·6	485·5
French Crab seedlings ..	0·2	8·6	7·4	31·6	94·9	101·5	189·8	434·0
M.II	5·1	29·4	39·4	86·5	101·3	146·0	154·4	562·1

Jonathan on M.I bore the heaviest crops for the first three years, followed by those on Spy for one year ; then the larger trees on M.XII took the lead and had, up to 1950, yielded considerably more fruit than the earlier cropping trees on M.I. The two semi-dwarfing stocks M.II and Spy gave similar yields.

Granny Smith on Malling II (Table VI) bore the largest crops each year except in the last, 1950, when trees on M.XII had the heaviest crop, but for the whole period tree on M.II were unsurpassed. Trees on Spy had crops very similar to those on M.II.

TABLE VI.

Granny Smith. Average crop per tree (lb.).

Rootstock	1943	1944	1945	1946	1947	1948	1950	Total
Spy	2·0	32·6	60·3	88·1	146·9	139·6	253·5	723·0
M.XVI	0·5	19·7	27·6	45·5	154·2	99·2	275·2	621·9
M.XII	0·2	9·0	20·8	36·6	162·1	114·7	302·1	645·5
Seedlings	0·7	12·6	26·9	30·4	106·3	86·7	213·0	473·6
M.II	1·9	38·4	65·3	89·0	166·3	150·1	276·0	787·0
M.XIII	—	2·7	16·9	15·0	70·3	79·4	136·2	320·5

Granny Smith on M.XII and M.XVI have yielded similarly, but Jonathan on M.XII carried a one-sixth greater crop. Both Jonathan and Granny Smith yielded poorly on Pomme de Neige seedlings.

Average number of fruits to the pound.

The comparative size of the fruits, as shown by this measure, is given in Table VII.

TABLE VII.

Average number of fruits to the pound.

Rootstock	1943	1944	1945	1946	1947	1948	1950	Average
	a. Jonathan							
Pomme de Neige seedlings	2·9	2·5	3·0	3·0	3·6	3·2	2·9	3·0
M.II	3·0	2·5	3·0	3·2	3·7	3·1	3·4	3·12
French Crab seedlings ..	—	2·7	3·0	3·0	3·8	3·2	3·4	3·18
Spy	3·1	2·5	2·9	3·2	4·0	3·3	3·4	3·2
M.XVI	3·0	2·8	3·2	3·2	4·3	3·3	3·8	3·37
M.XII	2·9	2·7	3·4	3·2	4·6	3·3	3·6	3·38
M.I	2·7	2·6	3·0	3·7	4·8	3·8	4·3	3·55
	b. Granny Smith							
M.XIII		2·5	2·5	2·5	2·6	2·4	2·2	2·45
Spy		2·3	2·6	2·4	2·7	2·4	2·4	2·46
Pomme de Neige seedlings		2·4	2·7	2·4	2·7	2·4	2·4	2·5
M.XVI		3·0	2·9	2·8	3·2	2·5	2·6	2·83
M.XII		3·0	2·8	2·8	3·0	2·6	2·7	2·82
M.II		2·7	2·6	2·6	2·8	2·4	2·7	2·63

There were only small variations in the average number of apples to the pound with each scion variety, but on the whole the Jonathan fruits were smaller than Granny Smith ; further, the order for fruit size on the different rootstocks is not the same for the two scions. With Jonathan, the fruits from the vigorous trees on M.XII and M.XVI were smaller than the fruits from trees on seedling stock. Hatton (1935) reports the occurrence of small fruits with Lane's Prince Albert on M.XII, the order for size of fruit being M.XVI > M.I > M.II > M.XII for this variety. Such differences in fruit size can be regarded as an expression of the mutual influence of rootstock and scion. Fruit from the heavy cropping trees of Granny Smith on Spy and on M. II compare favourably in size with those from trees on other rootstocks. The differences in the number of fruits to the pound are smaller than those found by Bryden (1948) at Bathurst, when using similar rootstocks and scions.

The small fruits of both scion varieties on all rootstocks in 1947 are probably due to a drought prior to harvesting the crop and not to the size of the crop ; there were heavier crops in later years but, despite this, the apples were larger than in the 1947 crop.

Effect of fertilizer treatments on growth and cropping.

Analyses of variance were carried out to test the main effects of the fertilizers on the crop weights 1943-48, the 1948 crop alone, and on the 1948 girth measurements. These showed no significant effects, but the girths of trees receiving the fifth treatment, i.e. no-superphosphate, were lower than the rest. An analysis of the 1950 yields confirmed this difference as significant, as shown in Table VIII.

TABLE VIII.

Effect of fertilizer on yield of Jonathan in pounds per tree, 1950.

	Fertilizer mixture	Mean log yield	Geometric mean (lb.)
	N P K		
1.	2 : 2 : 1	2·308	203
2.	4 : 2 : 1	2·208	161
3.	2 : 2 : 1 +2 : 0 : 0	2·182	152
4.	2 : 2 : 2	2·246	176
5.	2 : 0 : 2	2·058	114

Minimum difference between mean logarithms significant at 5%—0·116
1%—0·158
0·1%—0·214

DISCUSSION.

The relative order for vigour of growth induced by the rootstocks used in this trial is substantially the same as that found by Hatton (1935) for similar rootstocks with English scions, the order being M.XII > M.XVI > M.I or M.II.

As reported by Hatton above, there are scion partialities with rootstocks M.I and M.II, some varieties such as Cox's Orange Pippin being more vigorous on M.II than on M.I, while the reverse was the case with Lane's Prince Albert. In this trial, Jonathan trees on M.II are more vigorous than those on M.I, where growth is measured either by girth or by height and spread of tree.

At this comparatively early stage in the life of these trees, the usefulness of any particular rootstock and scion combination is a matter for a tentative forecast. It would appear that, for Jonathan trees, those on M.XII promise to outgrow and outyield any other combination in this experiment. The vigorous growth induced by M.XII stock has been shown by Hatton (1935) for other scions such as Lane's Prince Albert and Bramley's Seedling.

For Granny Smith, there appears the alternative of planting trees on Spy or M.II to secure an early return of capital, or using M.XII or M.XVI stocks and waiting a further number of years for these larger trees to overtake those on Spy or M.II in cropping, as in the case of Jonathan trees. One difficulty in the production of the Malling stocks is their susceptibility to woolly aphid attack in the nursery and, as has been noted at Stanthorpe, a delayed foliation in spring, which may affect the grafting of M.XII rootstocks; a small proportion of these have leafed-out as late as early December.

SUMMARY.

Twelve years after planting apple trees on clonal and seedling rootstocks, the largest and heaviest cropping trees are Jonathan on Malling XII rootstock. With Granny Smith as scion, the largest trees are on M.XII, but the heaviest crops have been borne by the trees on M.II and Northern Spy rootstocks to date. Trees on Pomme de Neige and French Crab seedling rootstocks are more variable in size than those on clonal rootstocks with both scions. The average weight of individual fruits shows small variations according to the stock used.

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SOME NOTES ON THE BIOLOGY OF THE APPLE SAWFLY, *HOPLOCAMPA TESTUDINEA* (KLUG)

By **G. H. L. DICKER**
East Malling Research Station, Kent

PRIOR to the investigations of Davies and Eaton (1950), who demonstrated that the Apple Sawfly could be efficiently controlled by BHC, it had been the practice in this country to apply a spray containing nicotine against this pest. Whilst good results were usually obtained, reports of failures were sufficiently numerous to suggest that factors other than bad spraying were operating. There appeared to be two main possibilities, either the timing of the spray application was incorrect or environmental conditions were reducing the efficiency of the insecticide.

Miles (1932) and Velbinger (1939) had already given a general account of the biology but observations by Massee (1944) that egg-laying sometimes occurred after petal-fall indicated that a more detailed study of the oviposition and hatching periods might help to provide an explanation of the occasional failures. The main work of the present investigation has thus centred upon these phases of the life cycle, with less extensive observations being continued to cover the whole period.

FLIGHT PERIOD OF THE ADULTS.

Methods.

Adult populations were estimated by tapping all accessible branches on a fixed number of trees and collecting the dislodged sawflies on a beating tray. Except in 1951, counts were made on the same plot at East Malling consisting of mature bush trees mainly of Worcester Pearmain, a midseason flowering variety which is usually most heavily infested ; only trees of this variety were sampled. At each date twenty-five trees, equally distributed over the plot, were tapped, there being six different sets of sample trees which were used in rotation. Similar methods were employed in 1951, using much smaller trees of the same variety on a nearby plot.

In order to avoid losses of this very active insect, all samples were taken between 6.30 and 8 a.m. or, when weather conditions made this impossible, beating was occasionally carried out at dusk. At neither period could adults be induced to fly. The large quantity of bud scales and petals falling on the tray made sorting an unduly tedious operation in the field, so only those adults immediately visible were counted at this time ; the others, together with all the debris, were placed in muslin bags and the contents later spread in large glass-topped boxes from which the adults were collected as they crawled to the surface. They were subsequently released on the plot.

Field observations.

Each year, as will be seen from Fig. 1, adults appeared in the sample collections soon after the first blossoms had opened ; numbers increased rapidly, reaching a peak within a day or two of full bloom, then declined. Compared with other years, emergence in 1950 was a little later in relation to the full blossom period. No sawflies were found on the trees before any open blossoms were present, or after petal-fall was complete, as observed by Massee (1944); occasional specimens, however, occurred in the late blossoms, especially those borne on two-year-old wood, after the 80 per cent. petal-fall stage had been reached.

Adult activity is closely related to weather conditions. It is greatest on still, sunny days; considerable movement also occurs when a breeze is blowing, provided that temperature and light intensity are high but, under dull, wet conditions, the sawflies show very little sign of activity. At night and when weather is unfavourable, the adults shelter among the blossom trusses; some hide in partly open blossoms, others beneath petals or the rosette leaves. Mating takes place in the blossoms.

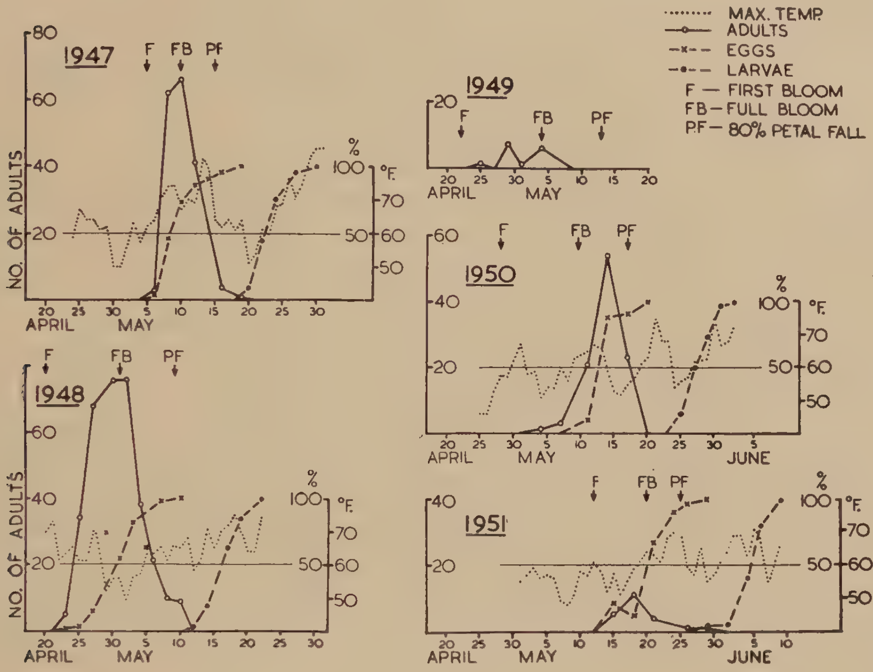

Fig. 1.

Graphs to illustrate the flight, oviposition and hatching periods of the Apple Sawfly, *Hoplocampa testudinea* (Klug), on the variety Worcester Pearmain, 1947-51.

The length of adult life under cage conditions in the laboratory extended to eighteen days, with an average of just over nine days for each sex, a figure in close agreement with 8·1 days given by Velbinger (1939). Assuming this to be correct also for specimens living in the orchard, it would seem from the graphs that populations often began to decline earlier than would be expected if natural mortality were the cause. There is thus some evidence to suggest a movement of sawflies from the trees shortly after full blossom, possibly because freshly-opened flowers are preferred for oviposition. Field observations support this suggestion because adults may often be seen on late-blossoming varieties after all the petals have fallen and sawflies can no longer be found on earlier varieties.

Sex ratio.

There was a marked difference in the proportion of the sexes during the years 1947-51. Males represented only 30 per cent. of the total captured by beating, the respective annual figures being 27, 30, 40, 23 and 32 per cent. Since there is evidence that the length of adult life of both sexes is the same, these figures can be taken as representing the actual proportion of the sexes occurring in the field. Similar results have been obtained from emergence cages beneath which fully fed larvae, collected from the orchard, were allowed to burrow freely into the soil ; of 52 adults recovered, 18 were males and 34 females. Velbinger (1939) observed an even greater excess of females among sawflies reared in cages but, from orchard collections, obtained 25 and 85 per cent. females in consecutive years. Downes and Andison (1942), working in British Columbia, recorded a preponderance of males, but their figures refer to individual catches and not to seasonal totals.

THE EGG-LAYING PERIOD.

Oviposition.

The elongate, translucent white egg is laid in the receptacle just beneath the base of the stamens. Within the tissue it is compressed laterally (Plate I, Fig. 1) but, on exposure, becomes oval and slightly curved (Plate I, Fig. 2). Normally the female takes up a position on the outside of the blossom and, with the ovipositor, makes an oblique slit, parallel to the base of the calyx, which does not quite reach through to the inner epidermis of the receptacle ; the egg is then deposited in this slit. Miles (1932) also observed females ovipositing in the reverse direction, i.e. the ovipositor was inserted from the inner side. Occasionally the saw enters at right angles to the surface and pierces the inner epidermis but no egg is then laid. A small drop of liquid exudes from the slit when the ovipositor is withdrawn and is often consumed by the female before she leaves the blossom. Slight traces of liquid, however, always remain and cause a rusty brown discoloration which provides a visual guide to the egg-laying site. As incubation proceeds, the egg swells considerably, at first forming a blister and finally rupturing the inner epidermis (Plate II, Fig. 1), so that before hatching takes place, the egg is always lying partly or completely exposed in the calyx cup. As a rule only one egg is laid in a blossom although, in the field, two are sometimes found and, very rarely, a blossom contains three ; under artificial conditions the number may be considerably greater. Eggs are almost invariably laid in open blossoms ; Massee (1950) reported oviposition in Worcester at the pink bud stage, an event of very rare occurrence in the writer's experience, and the same author (1944) observed egg-laying after petal-fall was complete. Kuenen and van de Vrie (1949) demonstrated that females would not oviposit in blossom clusters from which the rosette leaves had been removed and Velbinger (1939) obtained larvae from eggs laid by unfertilized females, showing that, in addition to the normal mode of sexual reproduction, parthenogenesis may also occur.

Oviposition under laboratory conditions.

An average of thirty-two eggs per female was obtained in the laboratory, considerably more than the average of thirteen obtained by Velbinger (1939). The cage consisted of a lamp-glass placed upon the surface of moist sand contained in a pot and enclosed with muslin at the top. Shoots with ten to fifteen open blossoms were changed daily and each cage contained only one pair of insects, the males being replaced if survived by the female. In 1947 and 1948 sawflies were collected from orchard trees on the first day adults were observed; those used in 1949 and 1950 came from emergence cages. Individual totals varied greatly, from five to one hundred and three eggs ; daily totals from single females exceeded ten eggs on eighteen occasions, the maximum laid by an insect in one day being twenty. The annual averages from 1947 to 1950 were 31, 54, 25 and 28 from 6, 4, 9 and 5 females respectively. Most females began laying on the day of emergence.

Field observations.

The progress of oviposition in the field was studied by collecting eight blossom trusses from each tree sampled for adults. The total sample was thus 200 trusses consisting of approximately 1,000 blossoms. These were first sorted according to the presence or absence of oviposition scars and the scarred blossoms were then dissected under a binocular microscope to detect the presence of eggs. During the full period of the investigation 88 per cent. of the scars were found to contain eggs. The graphs in Fig. 1 represent the number of eggs found in each sample, expressed as a percentage of the total in a similar sample at the end of the oviposition period ; very few eggs were seen in 1949 and these occurred so erratically that no satisfactory graph could be drawn.

With the exception of 1950, when emergence was later than usual, eggs were found on the same date as the first adults, thus confirming the laboratory observations that ovipositon begins very soon after emergence. The number of eggs increased rapidly during the main blossom period, at least 50 per cent. having been laid by the full bloom stage ; then the rate decreased until, at full petal-fall, adults were no longer present on the trees. A similar pattern was followed in 1950, only at a slightly later stage of the blossom period. These results agree very closely with those obtained in similar studies by Kuenen and van de Vrie (1949) in Holland.

THE HATCHING PERIOD.

Figures given by previous workers in this country show that the incubation period of the egg varies greatly, e.g. 10-18 days (Kearns, 1933), 8-10 days (Massee, 1933), 8-18 days (Miles, 1932), 13 days (Velbinger, 1939). Individual eggs were not studied during the present investigation but some general figures (Table I) may be obtained from the field sampling results illustrated in Fig. 1. It must, however, be borne in mind that the interval between successive samples was two or, more frequently, three days and, therefore, the periods quoted, especially those concerning the beginning and the end of both egg-laying and hatching are subject to slight error.

The main point brought out by Table I is the consistency of the figures during the four years under review. Only two diverge from the average by more than two days ; the interval of nineteen days between discovery of the first egg and observation of hatching in 1948 and the period of eight days which elapsed between 80 per cent.

TABLE I.

The hatching period, in days, in relation to oviposition and 80 per cent. petal-fall.

Interval	1947	1948	1950	1951
First egg to first larva	14	19	14	14
50% eggs laid to 50% hatch . .	14	15	14	15
Last egg laid to full hatch . .	11	12	13	11
80% petal-fall to first larva . .	5	3	8	4
80% petal-fall to 50% hatch . .	7–8	7	10	10–11
80% petal-fall to full hatch . .	15	13	16	15

petal-fall and hatching in 1950. There is considerable evidence to show that the latter was due to late emergence of adults but the former is not so easily explained. From Fig. 1, where the maximum daily screen temperature is plotted for the relevant periods, it would at first appear that the cool weather at the full blossom period was responsible, but this seems unlikely to be the cause as a corresponding delay in hatching did not accompany a period of similar temperatures in 1950, and the incubation period was not shortened by the consistently high temperatures in 1947. A more careful study of the initial stages of oviposition shows that the number of eggs increased very slowly compared with the rate of hatching over the corresponding period and this suggests that larvae hatching from the earliest-laid eggs were not included in the samples immediately hatching began.

Each year the hatching period was a few days shorter than the corresponding oviposition period, a phenomenon also observed by Kuenen and van de Vrie (1949), which indicates that temperature, whilst having no very marked effect, does hasten the development of the later-laid eggs.

The general picture obtained from Fig. 1 and Table I is that, following the 80 per cent. petal-fall stage, hatching normally began after four or five days, 50 per cent. of the eggs had hatched within ten days and hatching was virtually complete within fourteen days. The average incubation period, estimated from the 50 per cent. stage, was between fourteen and fifteen days.

THE LARVA.

Penetration of the fruit.

Shortly after hatching, the larva starts burrowing into the fruit. The tunnel usually begins within the calyx cup near the oviposition scar and is directed outwards, turning abruptly away from the calyx just before the epidermis is reached, then continuing a peripheral course which partly or completely encircles the fruitlet before becoming deeper and directed towards the core. In addition to the normal method of entry, from inside the calyx, tunnels are also found which have their origin on the surface of the fruit, indicating that young larvae sometimes crawl out of the calyx before beginning to burrow. Larvae are also occasionally observed mining the sepals, having turned in the direction opposite to the ovary after burrowing through the receptacle. The ribbon scars frequently observed on maturing fruits result from the superficial mines caused by young larvae which die early and fail to penetrate to the core. Having partly or completely consumed the seeds, the larva leaves the fruit and attacks another, entering in a radial direction from the side and burrowing directly to the core. Such fruits are recognised by the large entry hole around which accumulates a quantity of wet, reddish-brown frass. Damage involving the superficial tunnelling by newly hatched larvae is usually termed " primary " in contrast to the direct entry or " secondary " attack caused by migrating larvae.

Estimates of the number of fruits attacked by a single larva have been made by many observers but only Steer and Thomas (1935) give actual figures. These workers quote 1 : 1·17 as the ratio of primary to secondary attacks on fruit which means that whilst all larvae attacked two fruits, only 17 per cent. damaged three. During field trials on control measures complementary to the present investigation all drops were collected from mid-June onwards and the ratio was found to be 1 : 1·13, 1 : 1·00 and 1 : 2·00 in 1949, 1950 and 1951 respectively. Fruits penetrated by sawfly larvae and which have sustained damage or destruction to the seeds, cease growth and fall from the tree before or during the " June drop " period. Luckwill (1948) has shown that a hormone, governing abscission, is secreted by the seeds and the cessation of growth followed by abscission, associated with attacked fruits, is probably directly due to the destruction of these organs resulting in the removal of supplies of hormone.

Depth of the cocoon.

After feeding for about four weeks, the larvae reach maturity, leave the fruits and form cocoons in the soil, within which they remain in the prepupal stage until pupating three or four weeks before the adults are due to emerge. Miles (1932) found 75 per cent. of the cocoons at a depth of 3 to 9 in.; Hey and Steer (1934) obtained 89 per cent. from the top 4 in. and none below 9 in. In the present investigation mature larvae were placed on natural soil beneath a bottomless cage; approximately equal proportions of cocoons were recovered from the strata 0 to 3 in. and 3 to 6 in. below the surface, together representing 88 per cent. of the total; none occurred below 9 in.

Duration of the prepupal period.

Massee (1937) observed sawflies in orchards in 1936 which, due to severe frost damage, had borne no crop the preceding year; he concluded that reinfestation was due either to adults migrating from neighbouring orchards or to larvae remaining two years in the soil. Results obtained from observation cages have confirmed the findings of Velbinger (1939) that some larvae do spend two years in the prepupal or resting stage. From larvae put down in June, 1948, twenty-eight sawflies emerged in 1949 and ten in 1950; another batch of larvae collected in 1949 gave rise to one adult in 1950 and ten in 1951. No living larvae were found in cocoons beneath the cages after the second year although, from a small number collected in June, 1949, and kept in the laboratory, one was still alive in June, 1951. This date is later than the normal emergence period for adults and indicates that under certain conditions larvae may spend more than two years in the cocoon.

CONCLUSIONS.

From the foregoing observations it appears that the Apple Sawfly follows a very regular annual rhythm during the blossom period. Adults are attracted only to trees carrying open blossoms and, whilst eggs may be laid after 80 per cent. petal-fall, the number is quite small as will be seen from Fig. 1 where, each year, more than 90 per cent. of the total had been deposited by this stage ; oviposition ceases when open flowers are no longer present on the trees. The only departure from the normal occurred in 1950 when emergence was late, there being very few sawflies on the trees until the full blossom stage had passed, but even in this year all adults had died or had departed to later-flowering varieties by the time blossoming on the trees under observation had come to an end. Spraying against this pest does not begin until the 80 per cent. petal-fall stage and, in the majority of orchards all the petals have fallen before the spray is applied. Even where this is not so, the remaining petals are mostly removed by the forceful sprays now in common use. There does not, therefore, seem to be sufficient evidence to suggest that oviposition after spraying can account for past failures to control this pest. The effect of time of application in relation to oviposition and hatching is discussed by Dicker and Briggs (1953).

One other point merits attention ; namely that some of the larvae remain in the soil for two years. The figure of 40 per cent. obtained in emergence cages may not be representative of behaviour under natural conditions, but there is ample evidence to show that this phenomenon occurs and it is, therefore, essential, even with the very effective insecticides now available, to obtain adequate control during at least two consecutive seasons before any relaxation of measures against this pest is considered.

SUMMARY.

During observations extending over the years 1947-51 adults of the Apple Sawfly, *Hoplocampa testudinea* (Klug), were found on trees only when open blossoms were present. Emergence of the first adults normally coincided with the early stages of blossoming on the midseason-flowering variety Worcester Pearmain, and peak numbers occurred at full bloom ; males represented only 30 per cent. of the total population. Oviposition began very soon after emergence and from laboratory studies it is concluded that each female laid, on an average, 32 eggs. Larvae were first present about four days after 80 per cent. petal-fall, 50 per cent. of the eggs had hatched within the next six days and hatching was complete six days later ; some larvae remained in the soil for two years. Apart from later adult emergence in 1950, no marked differences in the annual life cycle occurred and it is considered unlikely that the occasional failure of control measures can be related to adult behaviour.

ACKNOWLEDGMENTS.

Mr. J. B. Briggs carried out all the excavations to determine the depth of cocoons in the soil. The photographs were taken by Miss Eleanor C. Thompson.

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PLATE I

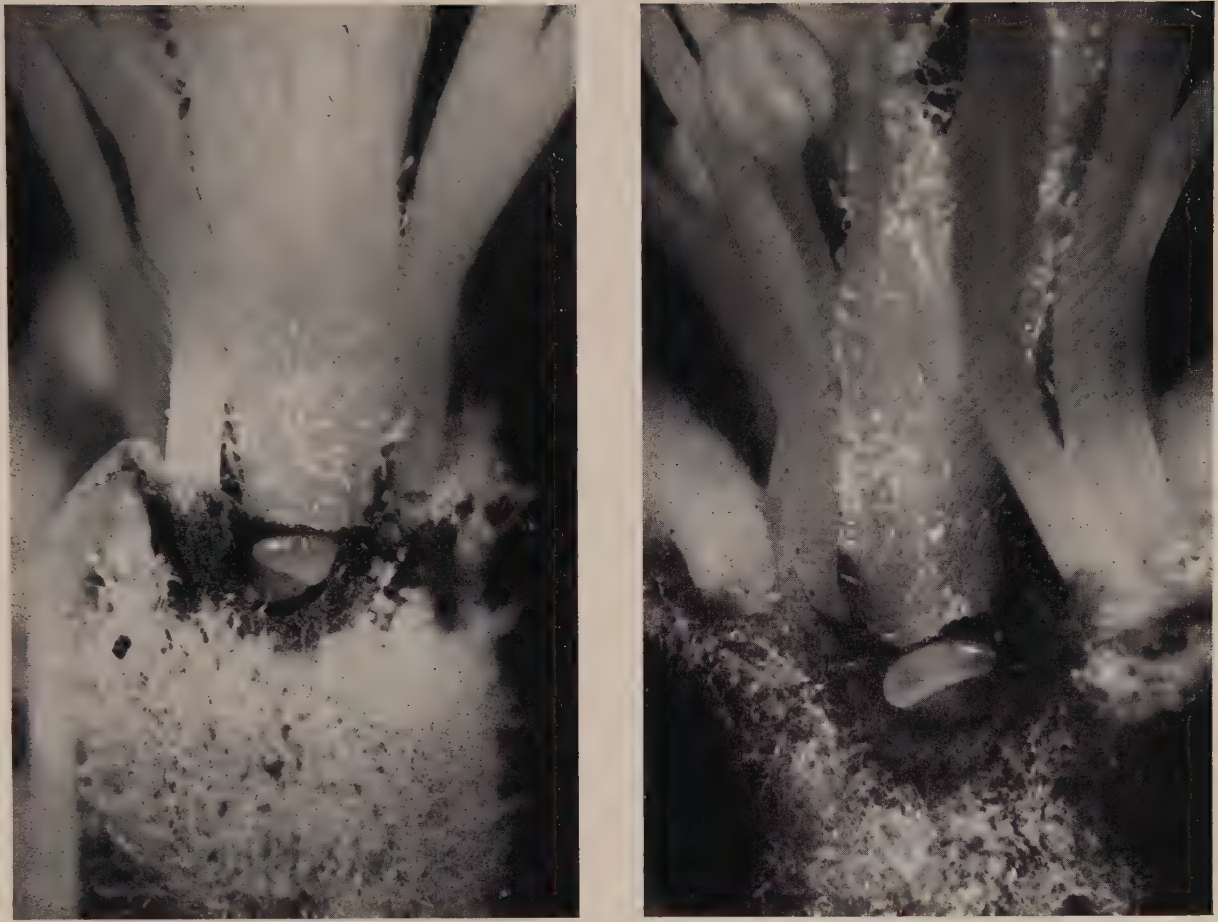

Fig. 1.

Fig. 2.

Portion of receptacle removed to show egg of Apple Sawfly, *Hoplocampa testudinea* (Klug); in oviposition slit (Fig. 1) and natural shape (Fig. 2) × 18.

PLATE II

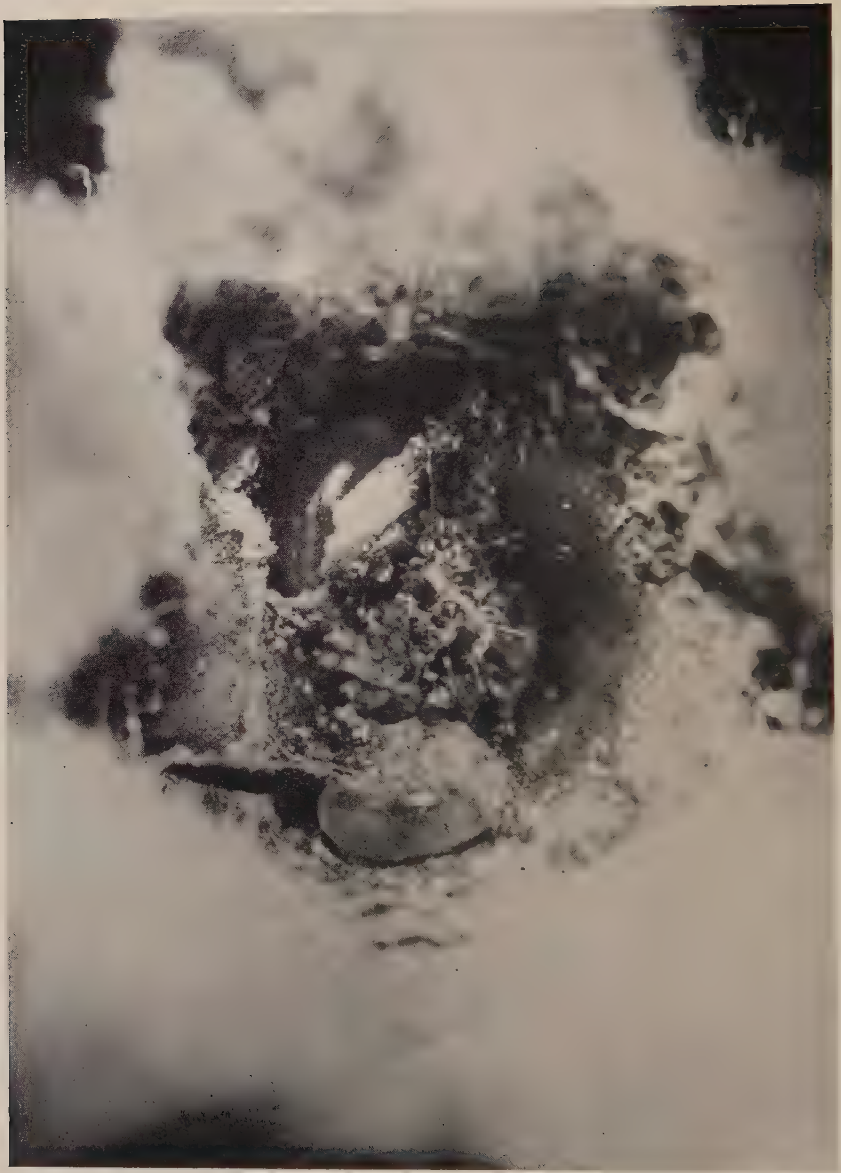

FIG. 1.

Calyx cup with stamens and style removed to show inner epidermis ruptured by swollen eggs of Apple Sawfly, *Hoplocampa testudinea* (Klug) × 23.

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BIOLOGY OF SOME PREDATORY INSECTS AND MITES ASSOCIATED WITH THE FRUIT TREE RED SPIDER MITE *(METATETRANYCHUS ULMI (KOCH))* IN SOUTH-EASTERN ENGLAND*

IV. THE PREDATOR-MITE RELATIONSHIP

By ELSIE COLLYER
East Malling Research Station, Kent

INTRODUCTION.

IN previous contributions to this subject (Collyer, 1952, 1953*a*, 1953*b*) the life histories of the predatory insects and mites have been described. It now remains to discuss the relative importance of the different species in relation to the Fruit Tree Red Spider Mite and to show, by comparing the fauna of neglected and commercial orchards, the many changes that have occurred following the intensive control methods employed in modern fruit growing. Evidence has been obtained to support the conclusions of other workers that the Fruit Tree Red Spider Mite has developed into a serious pest mainly as a result of modern sprays interfering with its enemies.

The value of natural enemies in reducing populations of red spider mites has been emphasized by many workers in various parts of the world; reports relating to *M. ulmi* and closely allied species having been listed by Groves (1951). With reference to the Fruit Tree Red Spider Mite, in Great Britain, Thompson (1939) and Cakebread (1947) have both referred to the control given by Anthocorids, and Hey (1944) and Austin and Massee (1947) mention control by *Blepharidopterus angulatus* (Fall.). In Germany, Andersen (1947) found that predators, the most important of which were *Orius minutus* (L.), *Anthocoris nemorum* (L.) and *Scymnus punctillum* Wei., gave a useful check to the mite populations in midsummer. Listo, Listo and Kanervo (1939) reported fourteen species attacking the mite in Finland of which they considered *Conwentzia pineticola* End., *Anthocoris nemorum* (L.), *Oligota flavicornis* Boisd., *Scymnus punctillum* Wei., and a species of Gamasid mite were of some importance. In Holland, Kuenen (1942, 1947) found that Anthocorids, *Scymnus minimus* Payk. and predacious mites were of value. Cottier (1934) found *Scymnus minutulus* Broun., *Arthrocnodax* sp. and a Gamasid mite in New Zealand, but reported that they became numerous too late in the season to give effective control. In the United States, Garman (1923) found that predators effectively controlled the mite every two or three years, and mentions three species of Thysanoptera, *Triphleps insidiosus* Say, *Stethorus punctum* (Lec.) and *Seius pomi* Parrott. At a later date (Garman, 1938; Garman and Townsend, 1938), in the same locality, *Scolothrips sexmaculatus* Perg., *Stethorus punctum* (Lec.) and *Seius pomi* Parrott were still considered the most important species and the effects of routine sprays on them were discussed. Houser (1928) found that *Stethorus punctum* (Lec.) sometimes gave a late control of the mite but was unreliable. Newcomer and Yothers (1929) found *Stethorus picipes* Casey, *Triphleps insidiosus* Say, *Scolothrips sexmaculatus* Perg. and *Seius* sp. of considerable importance in the Yakima Valley in August. Pickett, Patterson, Stultz and Lord (1946), working in Canada, drew attention to the need to consider spraying and its effects on the orchard fauna as a whole.

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* Part of a thesis approved for the Degree of Doctor of Philosophy in the University of London.

THE SPECIES OF PREDATORS PRESENT AND THEIR RELATIVE IMPORTANCE.

In a neglected orchard.

Although orchards of this type are rare nowadays in the fruitgrowing areas of South-East England, one has been available for study at Maldon in Essex. It consists of about four acres of mixed varieties of apples with a few plums and pears. The trees vary in age, are large and closely planted, have seldom been pruned and never sprayed. Underneath is a dense cover of brambles, nettles and other low-growing plants which,

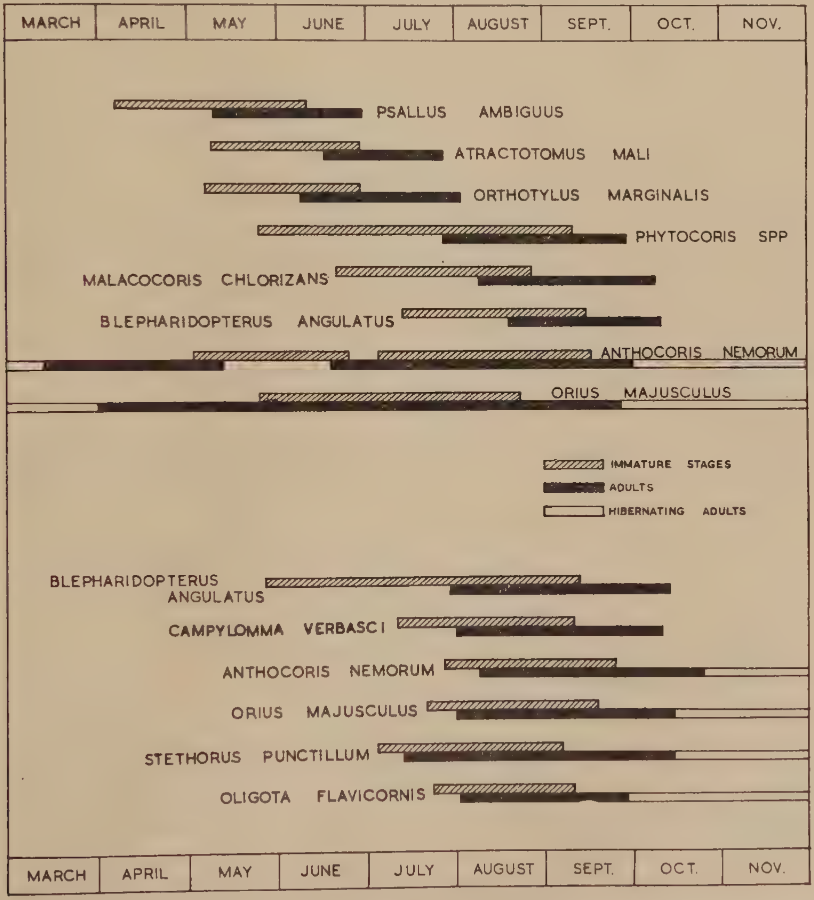

FIG. 1.

Occurrence of predators in a neglected orchard (upper) and a sprayed orchard (lower) in 1948.

on occasions, are partially cut back. The nearest commercial orchard is several miles distant.

Observations in this neglected orchard have extended over five years, and, during this period, populations of both predators and phytophagous mites have remained remarkably constant from year to year. Many different species occur but none in excessive numbers. As a typical example the main periods of activity of the more abundant species occurring in 1948 are illustrated in Fig. 1. These can be divided into two main groups.

(1) Species having only one generation a year, consisting of the Mirids, *Psallus ambiguus* (Fall.), *Atractotomus mali* (Mey.-D.), *Orthotylus marginalis* Reut., *Phytocoris* spp., *Malacocoris chlorizans* (Panz.) and *Blepharidopterus angulatus* (Fall.). In addition, *Camptobrochis lutescens* (Schill.) *Plagiognathus arbustorum* (F.), *Deraeocoris ruber* (L.) and *Campyloneura virgula* (H.-S.), not represented in Fig. 1, occur in lesser numbers. They are active in succession from early April until October, several species usually being present at any one time.

(2) Species of Anthocorid bugs which have two generations a year, all being present as adults or nymphs continuously from March until October ; the hibernating adults may also exhibit occasional activity during the winter. *Anthocoris nemorum* (L.) and *Orius majusculus* (Reut.) are most common with *Anthocoris nemoralis* (F.), *A. confusus* Reut. and *Orius minutus* (L.), occurring less frequently. Although having two generations a year, their density remains constant in this type of orchard as competition for food between the Anthocorids and Mirids is fierce.

Predacious mites of the family Laelaptidae behave very similarly to the insects in group (2) but have been omitted from Fig. 1, as it is difficult to compare their abundance or importance with that of the insect predators. Three species, *Typhlodromus tiliae* Oudms.*, *Typhlodromus finlandicus* (Oudms.) and *Phytoseius spoofi* (Oudms.) occur regularly in considerable numbers, feeding from May to October and occasionally also during the winter.

In commercial orchards.

Many sprayed orchards have been under observation and have shown great variability both in red spider mite and predator populations. The fauna consists of relatively few species, although the number of individuals may be very high, and populations are subject to violent fluctuations. The abundance of different species varies annually and also from orchard to orchard. Fig. 1 gives a general picture of the occurrence of predators in 1948 although it does not represent those present in any one orchard. Only the periods of greatest activity are indicated so all species except *Blepharidopterus angulatus* (Fall.), the Black-kneed Capsid, are represented only by the second generation when they become abundant.

The Black-kneed Capsid, the only Mirid which is numerous in both types of orchard, is the first predacious species to occur in appreciable numbers. The main hatch is in late June, or even later, by which time the red spider mite has reached the second generation. The other species, *Anthocoris nemorum* (L.), *Orius majusculus* (Reut.), *Stethorus punctillum* (Wei.), *Oligota flavicornis* Boisd. and *Campylomma verbasci* (Mey.-D.), although representing four different families, may be considered together. All pass through two generations, but only become important in commercial orchards in the second generation. These species become numerous in orchards only where high populations of the red spider mite are present. *C. verbasci* passes the winter in the egg stage, hatching in May and June ; the first generation is never numerous so it is not until July, when the second generation hatches, that the species becomes common. The other four species hibernate as imagines, many being killed by winter washes. Small numbers, however, either escape the winter sprays or fly in from neighbouring hedges in the spring and lay eggs during April, May and June, but it is only in the following generation that they attain importance. Where red spider mite infestations are severe these five species often become very abundant in August and September.

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* Nomenclature after Nesbitt (1951).

The Laelaptid mites are only occasionally numerous in commercial orchards. They are susceptible to sulphur, which is usually applied in spring and early summer, and are, therefore, only able to increase in late summer. *Conwentzia pineticola* End. does not appear in Fig. 1 as it was rare in the damp cool summer of 1948. In 1947 and 1949 it was, however, of importance and details of its spasmodic occurrence have been described elsewhere (Collyer, 1951). Even in years of abundance it does not appear in orchards until late July, but then increases very rapidly under favourable conditions.

THE EFFECT OF PREDATORS ON THE ACTIVE STAGES OF THE RED SPIDER MITE.

Various methods have been adopted in assessing populations of both adult and immature stages of the many predators and also of the red spider mite. Populations of the latter were estimated by the imprint method (Austin and Massee, 1947) except in the neglected orchard where the presence of other mites, e.g. *Bryobia praetiosa* Koch, made this method impracticable ; under these conditions a direct count was made with the aid of a binocular microscope. In each orchard, a sample of sixteen leaves was taken from each of eight randomized trees. Similar leaf samples examined under a binocular were necessary to obtain counts of all stages of the Laelaptid mites and eggs and larvae of *S. punctillum*, *O. flavicornis* and *C. pineticola*. Populations of all adult predators and the immature stages of those species not already mentioned were estimated by using a beating tray, four branches being tapped from each of eight trees in each orchard, different trees being sampled on each occasion a count was made.

In a neglected orchard.

In this type of orchard, winter eggs of the red spider mite always hatch earlier than in commercial orchards; in 1948 hatching started on 14th April, a week earlier than first noted in sprayed orchards. The mite has five generations during the summer months but, as illustrated in Fig. 2, the population remains low throughout the summer. This is due to two causes. Firstly, there are few winter eggs on the trees and, secondly, the predator-mite ratio is high throughout the period that living mites are present. Many of the predators which pass the winter as adults have already emerged from hibernation before eggs of the mite begin to hatch, e.g. the Anthocorid bugs, and these prey upon the immature forms of the first generation. As the season progresses, this group of predators is reinforced by a succession of other species and so a high population is always maintained.

Several other species of phytophagous mites occur in the neglected orchard of which *Bryobia praetiosa* Koch, *Brevipalpus geisenheyneri* (Rübs.), and *Eotetranychus*

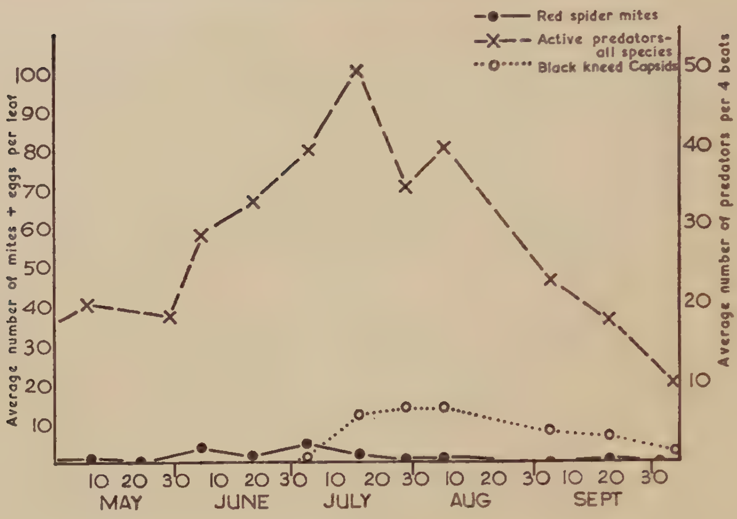

FIG. 2.

The Fruit Tree Red Spider Mite and its predators in a neglected apple orchard, Maldon, Essex, in 1950.

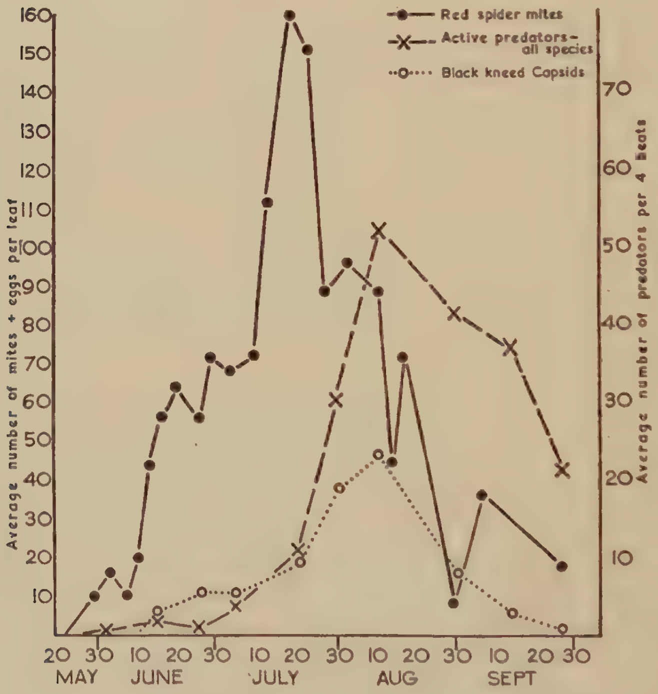

FIG. 3.

The Fruit Tree Red Spider Mite and its predators in a sprayed apple orchard, Great Braxted, Essex, in 1950.

carpini (Oudms.), are the most abundant. All these are also kept in check by the predators.

In commercial orchards.

The predator-mite relationship in well-kept commercial orchards varies greatly and is mainly dependent on the spray programme. It has already been pointed out that winter washes greatly reduce the population of species which hibernate as adults and so the initial spring population is nearly always low. In addition, sprays applied after the blossom period may have still more marked effects. Depending on the potential population of predators at the beginning of the season and the spray programme used, a complete range of effects may be obtained, from orchards in which predators keep the red spider mite below the level normally considered to be injurious, to those where the attack is so severe that premature defoliation occurs. Three examples are given to illustrate stages in this range :

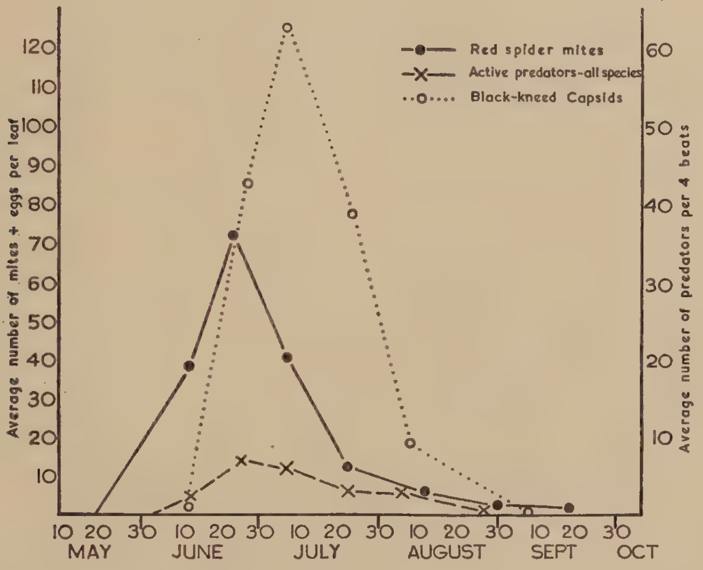

FIG. 4.
The Fruit Tree Red Spider Mite and its predators in a sprayed damson orchard, Boxted, Essex, in 1950.

(1) Illustrated in Fig. 3 is a commercial orchard which had many mite winter eggs and received routine tar oil wash in December, but no winter or summer acaricide. A severe infestation of mites followed, and this led to the development of many predators, chiefly *S. punctillum* and Anthocorid species. Immature stages of the Black-kneed Capsid were not very abundant in June, but many adults migrated in from neighbouring plots in late July and August, and laid eggs which gave rise to a large population in the summer of 1951. Damage occurred to the trees in July and August, but the predators so reduced the mites that very few winter eggs were laid.

(2) In another orchard (Fig. 4), again where mite winter eggs were plentiful, tar oil, but no acaricide, was used and the mites hatched in very large numbers. The Black-kneed Capsids which hatched in June were, however, sufficiently abundant to reduce the mite population almost immediately, and no economic mite damage occurred to the trees. The control of red spider mites was so complete that other predator species never increased, and some of the Black-kneed Capsids moved out in July and early August laying fewer eggs than were laid in the previous year.

(3) As a contrast to the above examples of predatory control, another orchard is considered (Fig. 5) where three applications of parathion during June and July caused a great initial reduction in mite numbers. All predators, however, were killed and, three weeks after the last application, a very rapid increase of mites started and leaf damage was visible before the end of August. A few predators, mainly Anthocorids and *C. verbasci*, began to establish themselves again only after this damage had occurred but were insufficient to prevent a very heavy winter egg population.

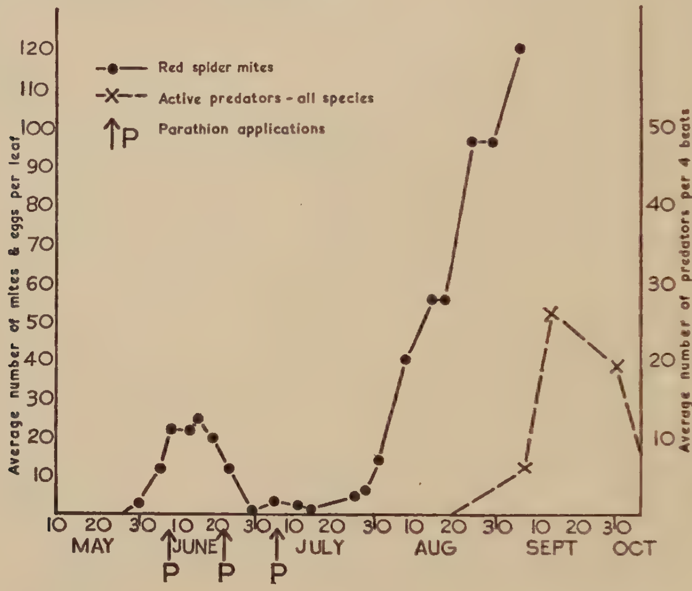

FIG. 5.
The Fruit Tree Red Spider Mite and its predators in a sprayed apple orchard, Hatfield Peverel, Essex, in 1950.

The four examples which have been quoted are of different orchards in the same year, but more knowledge of the course of natural control of the mite in commercial orchards can be obtained by studying the populations in the same orchard over a number of years, and this is now being undertaken in several locations where different spraying programmes are being used. As an instance, observations at one farm at Boxted, in Essex, have shown the sequence of mite populations when influenced mainly by one species of predator, the Black-kneed Capsid. A large population of this species was first noticed in 1947, following several years when mite populations had been high. In 1947 it reduced the mite population to a relatively low level in

July and maintained it there throughout the summer ; as a result there were many predator eggs in the winter and a fair number of mite eggs. In June, 1948, the predator was very abundant and reduced the mite populations to a very low level, which was maintained throughout the summer and, at the same time, the *B. angulatus* populations dwindled in the absence of a food supply. As a result, very few eggs of either the mite or *B. angulatus* were laid. In 1949 the few red spider mites which hatched built up rapidly, and by August the foliage of the trees was badly damaged, the few *B. angulatus* having had very little effect. These three years' observations were made in the absence of any acaricidal applications, the spraying programme being reduced to a minimum. In 1950 many mites were present in June, and predators were not numerous, so parathion was applied. The control achieved in 1947 and 1948 was of the type illustrated in Fig. 3 where *B. angulatus* so reduced the mite populations that other predators did not become numerous. The fluctuation between *B. angulatus* and the Fruit Tree Red Spider Mite over several years is typical of the interaction of a predator of this type and the mite (Nicholson, 1933), and shows that this species, on its own, cannot give an economic control of the mite for more than a few years at a time.

THE EFFECT OF PREDATORS ON WINTER EGGS OF THE RED SPIDER MITE.

Method of estimation.

For each estimation, ten representative young shoots are cut from the orchard and the total numbers of red and clear (i.e. sucked) eggs are then counted, with the aid of a binocular, on one inch of wood around the first wood bud of the last season's growth. Although this area may not have the same proportion of eggs attacked by enemies as the whole tree, it provides an index for comparison. On wood that is more than one year old, egg shells remaining from the previous season make any estimation inaccurate.

Two sources of error are unavoidable with this method of estimating the effect of predators on the winter eggs, and cause the percentage of sucked eggs to appear progressively less than it should be. Firstly, the empty egg shells tend to wear off the wood as the season advances. The second error arises from the different methods of feeding by the various predators. As the Hemiptera have haustellate mouthparts, and those of the larvae of *S. punctillum* and *C. pineticola* are also adapted for sucking, the empty shells always remain after these insects have been feeding, but the imagines of the latter two species have biting mouthparts and completely devour the eggs, leaving no evidence of their feeding.

In commercial orchards.

In this type of orchard, when both the red spider mite and its predators occur in large numbers in the autumn, the effect of predators on the mite winter eggs may be considerable. Results obtained in one orchard during the autumns of 1947 and 1948, which have already been discussed by Blair and Groves (1952), are illustrated in Fig. 6. Only percentages are represented, and it must be taken into account that the total numbers of eggs increased throughout the period starting from very few in August when the first winter eggs were being laid. The initial high proportion of clear eggs was due to the presence of very small numbers of hatched summer eggs which, being indistinguishable from sucked eggs, were included in this category.

The decreased percentage of clear eggs in early September in both years was due to oviposition by the fourth generation mites exceeding the rate of predation as at this time most of the predators were feeding on mites which were still plentiful on the leaves. As the fourth generation mites died in September, the rate of oviposition decreased ; at the same time there was a steady reduction in numbers of mites on the leaves, and predators began to move on to the wood where mite winter eggs were becoming abundant. This accounts for the increase in percentage clear eggs in late September of each year. In 1947 predators were very numerous and, despite the activity of the fifth generation mites in late September and October, their feeding exceeded the rate of mite oviposition, and the increase in percentage of clear eggs continued until 10th October, when *Anthocoris nemorum* (L.), *Orius majusculus* (Reut.), and *Stethorus punctillum* (Wei.) went simultaneously into hibernation. Of the important predators, only *Conwentzia pineticola* End. then remained in abundance. For a while, more eggs were deposited than were destroyed by the activity of this predator, but the activities of the predator become obvious as the last generation mites died off in the latter half of October. Larvae of *C. pineticola* were active until the end of December, by which time almost 90 per cent. of the eggs had been sucked. This high percentage of sucked eggs is not usual, only occurring when this species is particularly abundant. *C. pineticola* is spasmodic in its occurrence and was not present in 1948, so that after hibernation of the other predators, which occurred somewhat earlier and was more gradual than in the previous year, there was little predation.

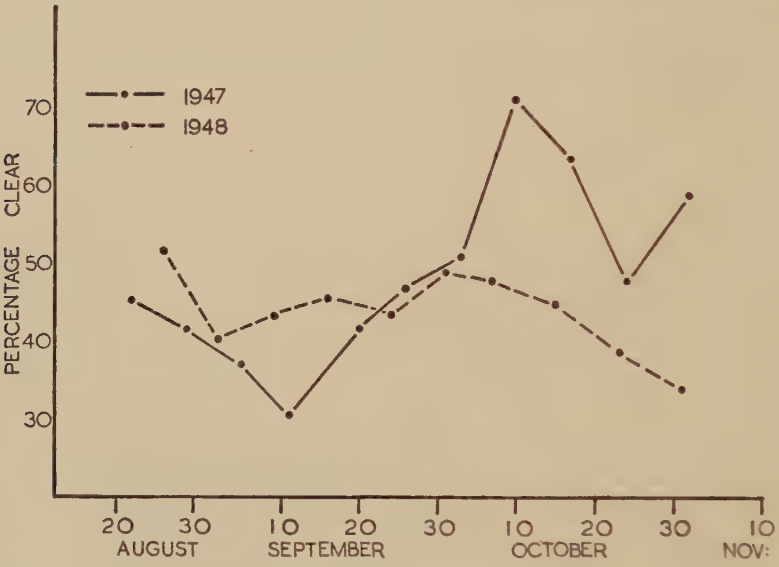

Fig. 6.

Percentage of winter eggs of the Fruit Tree Red Spider Mite sucked clear by predators.

Conditions vary so much in sprayed orchards that no estimate can be given of the percentage of winter eggs normally devoured by predators. The main period of predatory activity is in the autumn, but throughout the winter there is a gradual increase in the number of sucked eggs, and there is often another steep rise in the spring just before hatching begins.

The proportion of winter eggs sucked by the different species varies from year to year according to their relative abundance. Most predators prefer to feed on mites when these are available, which is usually until the leaves fall from the trees. *B. angulatus* and *C. verbasci*, the most abundant Mirids in sprayed orchards, die off by this time and so are responsible for the sucking of very few winter eggs. In captivity, with only winter eggs provided as food, *C. verbasci* feeds readily but *B. angulatus* rarely does so. *Camptobrochis lutescens* (Schill.), one of the less common Mirid species which hibernates as an adult, will suck many winter eggs. Other species which hibernate and often feed on winter eggs after the leaves have fallen, are *A. nemorum*, *O. majusculus*, *S. punctillum* and *Chrysopa carnea* Steph. Adults of the second and third generations of *C. pineticola* feed on winter eggs until the end of November, and larvae until the end of December; the Laelaptid mites when present also feed on winter eggs. *O. flavicornis* hibernates earlier than most of the other species, but feeds on mite eggs whilst still active. *Coccinella septempunctata* L., *Capsus meriopterus* (Scop.), adults of *Hemerobius* spp. and *Anystis agilis* Bks. are species which do not readily feed on winter eggs.

In neglected orchards.

In this type of orchard the total number of winter eggs is always low, and about 25 per cent. are generally sucked clear by predators by the end of November; predation then continues much more slowly until March and April, when there is renewed activity and, by the time hatching starts, about 40 per cent. have been destroyed.

FACTORS INFLUENCING PREDATOR POPULATIONS.

Cultural practices.

The great differences between the fauna of neglected and commercial orchards may be accounted for by several factors, and it is not possible to separate these effects from each other. The most obvious difference is the application of insecticides and fungicides, an aspect that will be considered in detail in a later paper, and many of the differences are obviously a direct result of sprays killing predators. Originally, the introduction of tar oil winter washes killed the hibernating Anthocorids and Coccinellids and, since then, the spraying programme has become more extensive and now plays a large part in determining the insect population of the trees. Less obvious factors must, however, be considered, as spraying cannot account directly for all the differences between the two types of orchard. The application of tar oil washes also has the effect of killing the growth of moss and lichen which is always present on neglected trees. These growths provide valuable protection for insects and their removal makes the tree a less favourable habitat for many predacious species. Many commercial orchards in Essex are cultivated whereas, in the derelict orchard, there is a dense undergrowth. It has been seen that most predators are not restricted to one host plant, and the low-growing vegetation provides an alternative source of food as well as excellent cover in windy or wet weather and also for hibernation. The absence of this cover in commercial orchards may be an important reason for the absence of some of the Mirid species several of which, including *Orthotylus marginalis* Reut., *Malacocoris chlorizans* (Panz.), *Phytocoris* spp. and *Deraeocoris ruber* (L.), are found very frequently in the summer on other plants in the neglected orchard.

Regular pruning removes many Mirid eggs, as most species oviposit in young wood. This factor is probably not very important as it affects all species, including *B. angulatus*, to an equal extent. The pruning and thinning of commercial trees keeps them limited in size, also open, admitting light and air. In the neglected orchard the trees are more closely planted, and very dense, excluding light and air ; the surrounding hedge and undergrowth accentuate this " housed-in " habitat, which presumably differs greatly in microclimate from that in commercial orchards, and may affect the fauna.

The balance of insect populations is delicate, and the changes which result from the factors that have already been considered give rise to further dependent differences. Spraying causes a reduction of predators and a related increase of red spider mites, and the environment thus becomes in two ways more favourable to incoming predators. There follows the great increase in numbers of certain predacious species, an increase never seen in the neglected orchard. Another difference which arises is the presence of certain species in sprayed orchards which occur only occasionally in unsprayed ones. Examples are *S. punctillum*, *O. flavicornis*, and *C. pineticola*, all of which have inactive soft-bodied larvae. Their scarcity in neglected orchards is either due to the fierce competition among predatory species which prevents the survival of these larvae, or the density of mites is insufficient to support them. *C. verbasci* likewise only occurs in commercial orchards where red spider mites are abundant, and probably increases in response to a favourable food supply.

Food preferences of the predators.

The abundance of the predators in commercial orchards depends largely on the spraying programme and is modified by cultural practices, but is also partially dependent on the feeding habits of the predators themselves. Some species, for example *S. punctillum*, *O. flavicornis* and *C. pineticola* feed only on mites, and enter the orchard and increase only when the mite infestation is already high. They follow the increase of mites but it is some time before they can overtake it and, when the mite population is falling, these species are the first to disappear. There are many species, including the Anthocoridae and non-phytophagous Miridae, which are general predators and feed on any available animal food, including their fellow predators. Although it might appear disadvantageous that they should feed on other beneficial species, this habit is actually of value in keeping the mite density low. The predators attack each other only when mites become scarce, and in this way a reduced population of predators remains, whereas, if they could not feed on each other, the whole population might die or move from the orchard. The predatory species thus maintains itself at a lower mite density than it could if the individual predators were wholly dependent on mites.

Some of the general predators are also partially phytophagous, for example *B. angulatus* and some other Mirids. The lower limit of mite population at which these species can survive is further reduced by their ability to feed on plant material. The extent to which the different predators are phytophagous varies, but the Mirids are unable to live on plant material alone, and some suck plant juices only occasionally. The predacious Laelaptid mites, however, appear to be able to live almost solely on plant material, at least towards the end of the summer, and can reduce the red spider mite population to a lower level than any other species without prejudice to themselves, and maintain it there. A few species feed on red spider mites only when other more favoured prey diminishes. The Coccinellids *Adalia bipunctata* (L.), and *Coccinella septempunctata* L. and members of the Chrysopidae, Hemerobiidae and Syrphidae are all attracted into orchards by outbreaks of aphids, but if, as a result of spraying or predatory activity, the aphids become scarce, the larvae of all these species feed on red spider mites. In this way a slight infestation of aphids in May and June may actually help in red spider control by attracting adults of these species into the orchards.

Rate of re-establishment.

Under commercial conditions the application of a spray material may suddenly reduce both predator and mite populations. The rate of increase of the mites is far greater than that of the predators, and it is not long before the population of mites previous to spraying is exceeded. *B. angulatus* has only one generation a year and, therefore, shows no immediate response to changes in mite populations, the significance of which has already been discussed. In contrast, the species with more than one generation like the Anthocoridae, Neuroptera, Coleoptera and the Mirid *C. verbasci*, can increase fairly rapidly when mite populations become high ; the potential rate of increase of each species depends upon the time taken to complete the life cycle, and the number of eggs that can be laid by each female. The development of a partial third generation by *Conwentzia pineticola* End. is important. The increase in density of these species results from a mite build-up but, whereas with *B. angulatus* there is a delay of a year, with these species an increase occurs in the same season and, even if too late to check the mite population on the leaves, the many predators devour a large percentage of the mite winter eggs.

Where constant spraying is practised, the ability of predators to reinfest the orchard from neighbouring unsprayed orchards, or hedges, ditches and woods, is of importance. The species most likely to invade the orchard from outside are those which live on other host plants and are active. The Anthocoridae usually reappear quickly, as they have a wide range of host plants and food organisms. *S. punctillum* behaves similarly, although restricted to mites for food. These species regularly reinfest winter-sprayed orchards each year. In contrast, *C. pineticola* feeds mainly on mites, and has no alternative host plants of importance in the neighbourhood of orchards in Essex. Consequently, when it leaves an orchard, there may be several years before it increases again, and then usually only in late summer. The Miridae are not very mobile and, although most of them occur on various hosts near orchards, only very small numbers move on to the fruit trees.

CONCLUSION.

The Fruit Tree Red Spider Mite is active and multiplying for many months from April until October. If adequate biological control in commercial orchards is to be maintained, it must be attacked by enemies throughout this time, as its potential rate of increase is so great. None of the insect predators has a life cycle similar to that of the mite, so it is probable that, in order to keep the mite population constantly low over many years, there is needed a succession of a number of species throughout the summer, as occurs on neglected trees. In sprayed orchards there is always a lack of predators in the early part of the summer after the winter sprays, or the alternative spring sprays which are now sometimes used, and this allows the early increase of the mite. Once this has happened the rate of re-establishment of the predators is important, a factor which is not involved on neglected trees. The variety of species on which the predators can feed is much reduced in sprayed orchards, and under these conditions they become more dependent on the red spider mite. All the predatory insects feed on active mites in preference to eggs and, after reducing the mites to a low density, may move away to find a more favourable food supply, leaving large numbers of mite summer eggs which subsequently hatch. The only predators which remain in unreduced numbers and feed on the summer eggs are the Laelaptid mites, which are also the only species with a life cycle closely resembling that of the red spider mite. It seems probable that, if any balanced state between red spider mites and predators is to be attained in orchards, these predacious mites must play an important part, together with a succession of insect species.

SUMMARY.

A comparison is made between the occurrence and relative abundance of predator species in an unsprayed, neglected orchard and in commercial orchards. The relationship between the predators and the Fruit Tree Red Spider Mite in these types of orchard is discussed, and several examples given of biological control of the mite which are compared with the control given by an acaricide. The effect of predators on winter eggs of the mite is described, and an account given of several factors which, in sprayed orchards, affect the predator populations.

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ZINC DEFICIENCY OF FRUIT TREES IN GREAT BRITAIN

By C. BOULD, D. J. D. NICHOLAS and J. A. H. TOLHURST
Long Ashton Research Station, University of Bristol

and

J. M. S. POTTER,
Director, National Fruit Trials, Wisley

In July, 1948, our attention was drawn to a serious failure of apple trees at the National Fruit Trials, Royal Horticultural Society's Gardens, Wisley, and we have been able to show that the main cause of the failure is an acute deficiency of zinc (2,3). Since then we have confirmed zinc deficiency in apples and other fruits, including pear, almond, cherry and ornamental crab, at other centres in the South of England by means of chemical and *Aspergillus niger* (M) soil tests, and by leaf and bark analyses. Control measures have also been tested, including foliage and dormant season sprays and stem and branch injection. It has been shown that zinc sulphate may be incorporated in the routine lime-sulphur sprays as a curative treatment.

Chandler *et al.* in 1931 were the first to recognize and correct zinc deficiency in fruit trees (7). Since then, the deficiency has been diagnosed in other fruit growing areas of America (5, 8), Australasia (4, 9, 10, 18), Africa (14, 15), and Europe (12, 16). The symptoms, which are usually well defined, are given descriptive names such as " little leaf ", " mottle leaf " and " rosette ", and are readily identified in apple, pear, stone fruits, walnut, grape, pecan and in *Citrus* fruits.

EXPERIMENTAL. WISLEY.

Site and soil.

The site is low lying and level, and the soil is a medium-coarse sand and gravel overlying deep gravel. A typical profile is as follows :

0-13 in. Dark brown medium sand, single grain structure, compact, with few medium sized stones.

13-48 in. Sharp change in colour at 13 in. to a yellow coarse sand, less compact, with increasing amounts of ½ to 1 in. gravel. This horizon is fairly moist with a water table at 48 in. (8.3.50).

The soil was acid until 1943 when 2 tons per acre of ground chalk were applied followed later by a further 2 tons per acre of dolomite. In 1948 the pH of the profile, from the surface to below 12 in., decreased with depth from 7·2 to 6·8. Further information is given in Table III.

Manuring and Cultivations.

Except during the war years the soil has received annually 2 cwt. of potassium sulphate and, every other year, 10 cwt. of hoof and horn meal per acre.

The orchard is under arable cultivation but from the end of June weeds are allowed to grow. These are disced in during late winter or early spring.

Trees.

The apple trees vary in size and age. The two varieties chosen for diagnostic work were Laxton's Pearmain on Malling Nos. I and II rootstocks, planted in 1930, and Edith Hopwood on Malling No. I rootstock planted in 1928-29. Other varieties in the orchard at Wisley showing zinc deficiency symptoms are Opalescent, Gloucester Cross, Lord Hindlip, Lord Peckover, Exquisite, Bowhill Pippin, Herring Pippin, Gladstone, Rosy Blenheim, Betty Gunningham and Newport Cross. The deficiency has been recorded on trees growing on all three rootstocks used in the trials, namely Malling Nos. I, II and XII. Of the varieties mentioned, the worst affected are Laxton's Pearmain, Edith Hopwood and Lord Hindlip.

Symptoms.

In apple trees the first symptoms appear at the time of flowering. The affected shoots carry sparse foliage and show typical short internodal growths with leaf rosetting and shoot die-back. (This is a winter die-back not to be confused with the summer die-back due to copper deficiency.) The leaves are much reduced in size and tend to be lanceolate, with wavy margins and diffuse intervenal chlorosis often with a narrow dark-green marginal rim (See Plate I). Under mild deficiency conditions the leaves may not be reduced in size and may show only a general intervenal chlorosis. Shoots and spurs are markedly brittle and the bark of older growths may be somewhat rough. As the trees were also low in copper this last named symptom may not be entirely due to zinc deficiency.

It is unusual for the whole tree to be affected. Certain branches may show deficiency effects whilst others on the same tree appear normal. Fruits on affected spurs are much reduced in size.

In pear the symptoms are not so clearly defined as in apple. The leaves are much reduced in size, with a tendency for the edges to curl upwards but without the marginal waviness shown by apple. Pear leaves may also show a diffuse intervenal chlorosis (See Plate II).

Apple and pear trees that are severely affected by the deficiency are stunted and make little extension growth. This is in marked contrast to trees suffering from copper deficiency which make vigorous growth until July, then develop die-back.

Treatments.

A visual diagnosis of zinc deficiency was made in late June and the first confirmative treatments were given on 6th July, 1948. These included foliage sprays and solid injections of zinc, manganese and copper sulphates, singly and in combination.

Foliage sprays were applied on a branch basis, using A.R. salts in distilled water and an all-glass spray equipment. Each treatment was replicated three or four times. The concentrations used were :

Zinc sulphate ($ZnSO_4.7H_2O$)	0·15% 0·30% + 0·15% calcium hydroxide ($Ca(OH)_2$)
Manganous sulphate ($MnSo_4.H_2O$)	0·15% 0·30%
Copper sulphate ($CuSO_4.5H_2O$)	0·10% 0·30% + 0·15% calcium hydroxide
Combined salts each at	0·10% + 0·15% calcium hydroxide

The solid salts were also injected into branches using one fifth and half the rates recommended by Bennett (1) for ferrous sulphate in the treatment of lime-induced iron chlorosis.

In February, 1949, some trees of the variety Laxton's Pearmain were given a dormant spray using zinc sulphate solutions at 4 per cent. and 2 per cent. respectively.

During the second week of June the orchard outside the experimental area was given a foliage spray of zinc sulphate at 0·2 per cent. concentration, using routine orchard equipment. Certain varieties of apple and pear were more susceptible to spray damage than others. Further information on this point is given later.

EXPERIMENTAL. OTHER CENTRES.

Zinc and copper deficiencies have been found in fruit growing on other soils derived from the Greensand and Corallian formations, and on coarse alluvial deposits. These have been confirmed by soil and leaf analysis but no corrective treatments have been applied.

RESULTS. WISLEY.

Visual response to treatments. 1948.

There was very little response to treatments during 1948, but a few rosettes that had received foliage sprays of zinc sulphate alone, or in combination with copper and manganese, made new leader growths with normal green leaves. In no instance did copper or manganese, alone or in combination, produce any beneficial effect on the rosettes.

Solid injection of zinc sulphate alone had no effect on symptoms or growth in 1948.

On some trees, zinc sulphate at 0·15 per cent. concentration caused slight defoliation. The spray damage was reduced by the addition of calcium hydroxide. The defoliation may have been accentuated by the low magnesium status of the leaves. Concentrated zinc sulphate sprays when applied during the dormant season caused no damage to the trees.

Residual effects. 1949.

The effect of the zinc treatments applied in 1948 was noticeable as soon as growth commenced and became more pronounced at flowering. The branches that had received zinc sulphate sprays grew vigorously and the leaves were dark green and normal in size. This is illustrated in Plate II (Fig. 3).

The growth on branches that had been injected with zinc sulphate was variable. Some spurs produced normal growths and leaves, whilst others still showed signs of chlorosis.

Trees given a concentrated zinc sulphate spray during the dormant season produced normal growth. In no instance did copper or manganese treatments have any effect on rosetting.

Spray damage.

Varieties differed in their susceptibility to spray damage. On some varieties damage was limited to scorching of foliage but, in those most susceptible, defoliation occurred. Details for apples and pears are given in Tables I and II. It should be borne in mind that the trees at Wisley have a low magnesium status and may have been more liable to damage.

Chemical data.

Chemical data on soil from an area at Wisley showing zinc deficiency are given in Table III. Zinc was determined by the method of Holmes (11). Further information on other soils with particular reference to their available zinc content, as determined by the *Aspergillus niger* method (17), is given in Table IV.

Table V shows the zinc content of healthy and deficient samples of leaves and bark from various fruits, and Table VI the zinc content of apple leaves after zinc treatments.

DISCUSSION.

The results of soil and plant analyses, together with the response to zinc sulphate sprays and injection, show conclusively that the trees at Wisley and at other centres were suffering from an acute zinc deficiency. The soil at Wisley is very low in available zinc which may have been further reduced in recent years by applications of limestone. The results in Table IV indicate that when the available zinc in the soil, as determined by the *Aspergillus niger* method, falls below 5 μg. Zn per gm. (p.p.m.) in

TABLE I.

The effect of foliage sprays of zinc sulphate, at 0·2 per cent. concentration, on apples. Spray applied during the second week of June, 1949.

Variety	Extent of damage	
	Scorching	Defoliation
Apple		
Allington Pippin		Medium
American Mother		Slight
Annie Elizabeth		Slight
Bachelor's Glory		Slight
Baumann's Red Reinette	Slight	
Beauty of Bedford		Slight
Bietigheimer Red		Trace
Black Prince		Medium to Severe
Calville des Femmes		Very slight
Christmas Pearmain	Slight	Slight
Coxstone		Medium
Edwin Becket		Trace
Green Harvey	Slight	
Gulval Seedling		Trace
Hambling's Seedling		Trace
Imperial		Trace
New Hawthornden	Slight	
Ohinemuri		Slight
Red Joaneting		Slight
Sandlin Duchess		Trace
Schofageable		Slight
Upton Pyne		Slight

TABLE II.

The effect of foliage sprays of zinc sulphate, at 0·2 per cent. concentration, on pears. Spray applied during the second week of June, 1949.

Variety	Extent of damage	
	Scorching	Defoliation
Pear		
Bergamotte d'Heimbourg		Slight
Beurré Bosc		Slight
Beurré d'Arenburg		Medium to severe
Beurré de l'Assomption		Medium
Beurré Diel		Very slight
Beurré Dubuisson		Very slight
Beurré Mortillet		Slight
Beurré Rance		Medium
Calebasse Grosse		Very slight
Chaumontel	Severe	
Dana's Hovey		Severe
Doyenné d'Alencon		Trace
Duchess d'Angoulême		Slight
Durondeau	No damage	
Early Market	Severe	Slight
Fondante d'Automne		Slight
Fondante de Thirriott		Slight
General Todleben		Trace
Huyshe's Victoria		Slight
Josephine de Malines		Severe
Knight's Monarch		Trace
Marguerite Marillat	Leaf tips twisted and scorched	
Packham's Triumph		Trace
Passe Crasanne		Slight
Phelp		Medium
*President d'Osmanville		Medium
Record	Severe	Slight
Sir Harry Veitch	Severe	Slight
*Summer Beurré d'Arnberg		Slight
Thompson's		Medium
White Doyenné		Medium

* One of the two trees of the variety, unaffected, showed no damage.

TABLE III.

Chemical data for soil from an area at Wisley where fruit trees showed severe zinc deficiency.

Depth	pH	Organic matter*	P_2O_5% in 1% citric acid	μg. Zn per gm. of soil (p.p.m.)			
				Exchangeable Zn N. neutral ammonium acetate method	Zn soluble in N. ammonium acetate adjusted to pH 4·5	Soluble in cold N/10 Hydrochloric acid	*Aspergillus niger* method
0–6 in.	7·2	1·29	0·059	1·31	8·9	10·2	1·5
6–12 in.	7·0	0·83	0·030	0·74	2·9	4·0	0·5
12 in +	6·8	0·45	0·022	0·90	2·7	3·6	—

* Organic carbon × 1·724.

Table IV.

The available zinc of soils as determined by the Aspergillus niger *method.*

Location	Depth of soil sample in.	Zn as µg. per gm. air-dry soil (p.p.m.)	Zinc deficiency in fruit trees
Wisley (Surrey)	0–6	1·5	Severe
Wisley ,,	6–12	0·5	,,
Wisley (Surrey)	0–6	4·0	Slight
Wisley ,,	6–12	2·0	,,
Wisley (Surrey)	0–6	9·0	Absent
Wisley ,,	6–12	4·0	,,
Faversham (Kent)	0–6	10·0	Absent
Faversham ,,	6–12	6·0	,,
Milbury Heath (Gloucestershire)	0–6	12·0	Absent
Milbury Heath ,,	6–12	8·0	,,
Long Ashton (Somerset)	0–6	30·0	Absent
Long Ashton ,,	6–12	20·0	,,

Table V.

The zinc content of healthy and deficient leaves and bark of fruit trees.

Fruit and location	Plant part analysed	Zn as µg. per gm. dry matter	Symptoms
Apple			
Laxton's Pearmain (Wisley)	Leaf	9·6	Normal from deficient tree
Laxton's Pearmain ,,	,,	1·2	Little leaf and rosetting
Edith Hopwood ,,	,,	2·3	,, ,, ,, ,,
Edith Hopwood ,,	,,	1·6	,, ,, ,, ,,
Hereford Cross ,,	,,	3·0	,, ,, ,, ,,
Lord Hindlip ,,	Bark	10·8	Normal from deficient area
Lord Hindlip ,,	,,	2·1	Little leaf and rosetting
Cellini Pippin ,,	Leaf	25–55	Normal
Crane's Seedling ,,	,,	6·1	Chlorosis and slight rosetting
Lane's Prince Albert (L. Ashton)	,,	18–30	Normal
Edward VII ,,	,,	20–24	,,
Worcester Pearmain (Cannington)	,,	20–55	,,
Laxton's Superb ,,	,,	25	,,
Pear			
Conference on Quince (Gloucester)	,,	22–23	,,
Crab			
Veitch's Scarlet (Exeter)	,,	14·1	Little leaf
Veitch's Scarlet ,,	,,	15·4	Chlorosis only
Cherry			
Sweet Cherry (Holland)	,,	13·0	Rosetting
Morello Cherry (Exeter)	,,	17·6	Slight rosetting
Almond			
Variety not known (Exeter)	,,	41·5	Normal
Variety not known ,,	,,	21·6	Little leaf

TABLE VI.

The effect of spray treatments on the zinc content of apple leaves, var. Laxton's Pearmain, *previously zinc deficient. (Zinc content <10 μg. per gm. dry weight prior to spraying).*

Treatment	Date applied	Sampling date	Total zinc as μg. per gm. dry weight
4% Zinc sulphate, dormant spray	16.2.49	4.9.50	24·8
2% Zinc sulphate, dormant spray	16.2.49	4.9.50	26·6
0·1% Zinc sulphate in 1/100 lime-sulphur ..	2.5.50	4.9.50	20·6
0·1% Zinc sulphate in water	2.5.50	4.9.50	24·9

the top 6 in. of air-dry soil, the trees are liable to suffer from zinc deficiency. When the value is as low as 1 to 2 p.p.m. the deficiency becomes severe. A normal soil contains more than 10 p.p.m. of available zinc.

Plant analyses also differentiate between normal and zinc-deficient trees. In apple, from July onwards, the threshold value appears to be about 10 p.p.m. of zinc in the dry matter of leaves and bark. When the value falls to 5 p.p.m. or less, "little leaves" and "rosettes" appear and the trees become stunted. The threshold values for cherry and almond may be higher than for apple although there are insufficient data to confirm this point. There is no evidence of any rootstock effect in relation to zinc deficiency at Wisley.

The deficiency is easily remedied by foliage or dormant sprays. Foliage sprays of 0·1 per cent. zinc sulphate plus a wetting agent should be applied at petal-fall or shortly afterwards. If they are applied after the end of July it is unlikely that the symptoms will be corrected in the same season, but sufficient zinc will be absorbed to correct the deficiency in the following year.

Trials indicated that zinc sulphate is equally effective when mixed with lime-sulphur sprays, but the precipitate of zinc sulphide must be kept in suspension by agitation, and a wetting agent must be used.

Varieties are likely to differ in their susceptibility to damage from foliage sprays, and this damage may be increased if other nutrients are deficient. When damage is likely it will be preferable to use a dormant season spray (zinc sulphate at 4 or 5 per cent.).

Injections of solid zinc sulphate into the trunk and branches will correct the deficiency but the method is tedious and liable to cause local damage to the tissues.

SUMMARY.

1. Zinc deficiency symptoms in apple and pear are described and illustrated.

2. The threshold level for zinc in apple leaves and bark, coinciding with the onset of visual symptoms, is about 10 μg. Zn per gm. dry matter. Severely affected leaves contain less than 5 μg. Zn per gm. dry matter.

3. Normal soils contain more than 10 μg. of available Zn per gm. air-dry soil as determined by the *Aspergillus niger* method. Soils containing less than 2 μg. of available Zn per gm. air-dry soil will induce deficiency symptoms in fruit trees.

ZINC DEFICIENCY OF FRUIT TREES IN GREAT BRITAIN
BY C. BOULD, D. J. D. NICHOLAS, J. A. H. TOLHURST AND J. M. S. POTTER.

PLATE I

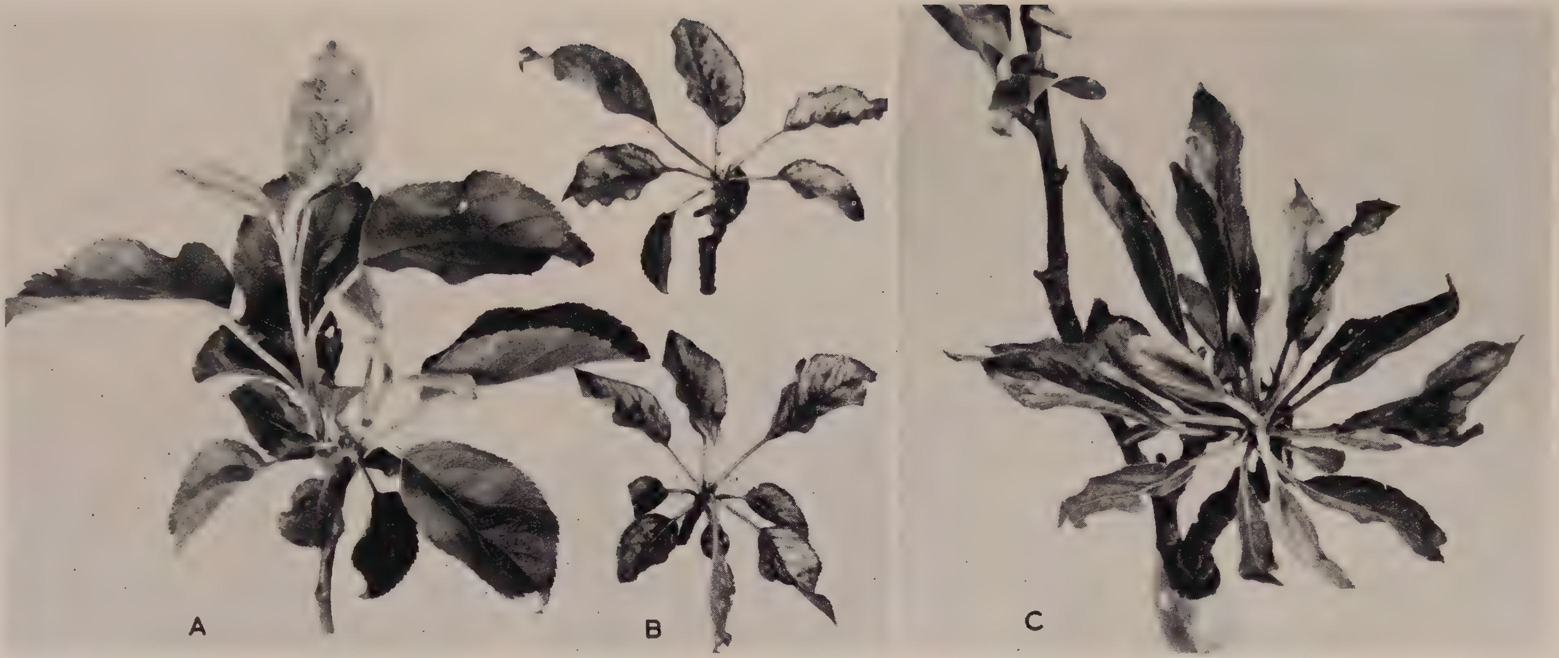

FIG. 1.

A. Normal shoot ; *var*. Edith Hopwood.
B. Zinc-deficient shoots ; *var*. Edith Hopwood. Note rosetting, upward curling and waviness of leaf margins, and intervenal chlorosis.
C. Rosetted shoot; *var*. Laxton's Pearmain.

PLATE II

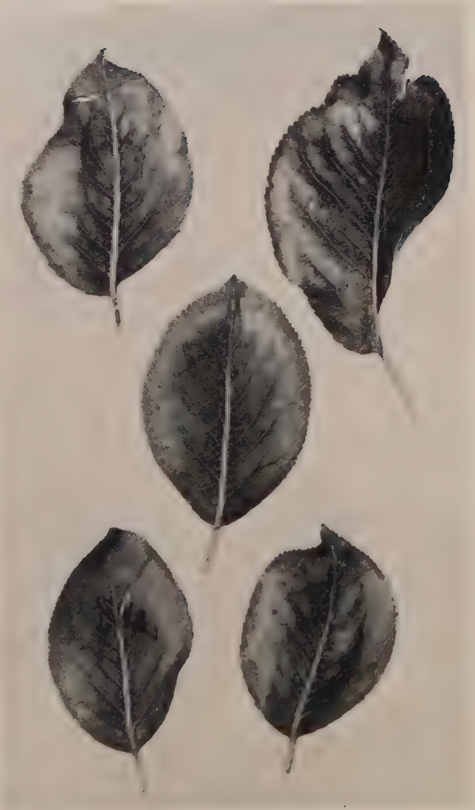

FIG. 2.

Zinc deficiency in pear; var. Bristol Cross. Showing diffuse intervenal chlorosis.

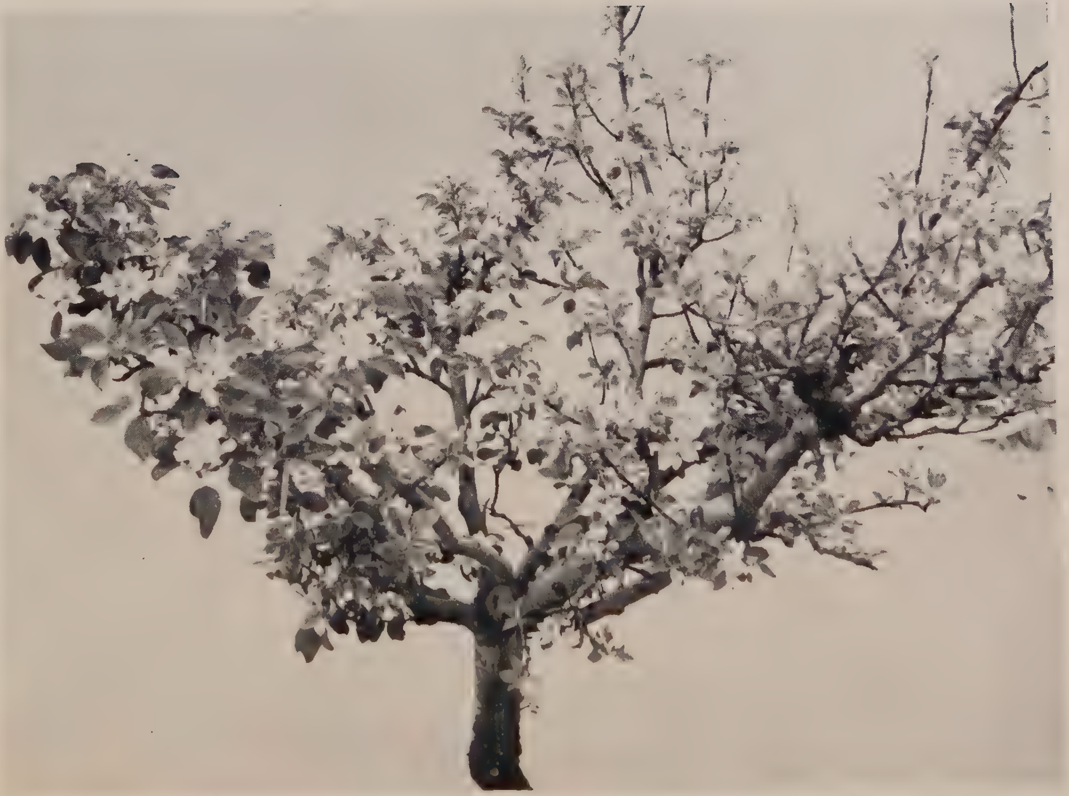

FIG. 3.

Response to zinc treatment: apple var. Edith Hopwood. Branches on left sprayed with 0·15% zinc sulphate in July 1948; photographed in spring 1949.

4. Zinc deficiency in fruit trees may be corrected by foliage sprays of 0·1 per cent. zinc sulphate at petal-fall, or by 4 to 5 per cent. zinc sulphate sprays during the dormant season.

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COPPER DEFICIENCY OF FRUIT TREES IN GREAT BRITAIN

By C. BOULD, D. J. D. NICHOLAS and J. A. H. TOLHURST
Long Ashton Research Station, University of Bristol

and

J. M. S. POTTER
Director, National Fruit Trials, Wisley

FLOYD was the first to show that a die-back or " exanthema " condition in citrus was corrected by the application of copper salts either as soil treatment or foliage sprays (7). Since then copper deficiency has been observed in apple (1, 2, 3, 6, 16), pear (1, 2, 3, 9, 13), plum (4, 14), prune, olive, avocado (15, 16) and tung (5). The world distribution of the deficiency follows closely that of zinc deficiency, occurring in America (5, 8, 13, 15, 16), Africa (1), Australia (4, 6, 10, 14) and more recently in Britain (2, 3, 9).

During the 1948 season when experiments on the correction of zinc deficiency were in progress at Wisley, we observed " summer die-back " in shoots of apple and pear. These were similar to the symptoms of copper deficiency described previously by Anderssen (1), Oserkowsky and Thomas (13) and Dunne (6). In preliminary publications (2, 3) it was shown that the disease is caused by an acute deficiency of copper. This is the first record of the deficiency in fruit trees in Britain, although cereal crops in East Anglia are known to suffer from copper deficiency (12). Jones (9) has also shown that a die-back condition of pear in Kent can be corrected by foliage sprays of copper sulphate. Muskett (11) suggests that the use of Bordeaux mixture as a fungicide, since 1924, in apple orchards in Northern Ireland may have corrected copper deficiency and resulted in vigorous tree growth.

This paper amplifies a previous report on copper deficiency in apple and pear at Wisley (*loc. cit.*) and records the condition on some sandy soils in Southern England. Affected fruits include almond, peach and cherry. It is shown that foliage sprays of 0·05 per cent. copper sulphate and of Bordeaux mixture applied at petal fall, soil applications and injections of solid copper salts will correct the deficiency. Chemical analysis showed that the copper content of leaves from deficient trees was below 5μg. per gm. dry matter, whereas leaves from healthy trees showed values of 5 μg. or above. *Aspergillus niger* soil tests suggest that the deficiency is likely to occur in fruit trees when values are below 2 μg. per gm. air-dry soil.

EXPERIMENTAL. WISLEY.

The site, soil, trees, manuring and cultural conditions have been described in a previous paper (*J. hort. Sci.* **28**, p. 260). Several varieties of apple and pear were observed to be suffering from summer die-back, including the apples Gloucester Cross, Hereford Cross, Cellini Pippin and Crane's Seedling and the pears Bristol Cross and Beurré Bedford all of which were used for experimental purposes. Apples on Malling

No. XII rootstock were more severely affected than those on M.I and M.II rootstocks.

Symptoms.

In apple, the first symptoms appeared in early July on the terminal leaves of the current-year shoots as large irregular necrotic areas accompanied by upward curling and distortion of the leaves. The lower leaves on affected shoots were usually pale green and lustreless and frequently showed numerous small irregular necrotic areas. One variety, Crane's Seedling No. 304, in addition to these symptoms, showed a diffuse intervenal chlorosis, but this was not usual. Towards the end of July, defoliation of the shoots occurred, progressing basipetally, and from September onwards they withered and died (See Plate I), hence the names " wither tip " and " summer die-back ". In older trees, when the deficiency was severe, the bark of the main branches and trunk became very rough and deeply fissured. This was followed by localized death and shedding of bark tissues, and profuse sucker development from the basal portions of the tree. These shoots were vigorous at first but later showed the typical leaf symptoms and die-back condition (See Plate II, Fig. 2).

In pear the symptoms were similar to those in apple. The terminal leaves on current-year shoots were the first to be affected. The leaf tips first became yellow and this stage was followed rapidly by necrosis (See Plate III, Fig. 3a). Later in the season most of the new shoots developed die-back almost to their origin ; the dead terminal leaves often remained but the lower leaves fell off. The dead shoots became black in colour.

Experimental treatments.

In Experiments 1 to 6, A.R. copper sulphate, $CuSO_4.5H_2O$, and Bordeaux Mixture, 4:4:50 were the copper compounds used unless otherwise stated. A spreader was incorporated in all foliage sprays other than the Bordeaux mixture.

Experiment 1.—In July, 1948, two apple trees *var.* Gloucester Cross, growing as half standards on M.XII rootstock, were selected for treatment. These two trees were chosen because they had suffered from severe die-back for several years and other trees on this rootstock in the immediate neighbourhood had already died. On 6th July, 1948, certain branches were sprayed with a 0·1 per cent. of copper sulphate and others were injected with solid copper sulphate at one fifth of the ferrous sulphate rate used in the treatment of lime-induced iron chlorosis.

Experiment 2.—On 16th February, 1949, eight large bush apple trees, *var.* Crane's Seedling No. 856 on M.XII rootstock, were given the following treatments in duplicate :

1. Control—no copper sulphate.
2. Soil application, $\frac{1}{2}$ lb. commercial grade copper sulphate broadcast round each tree.
3. Trunk injection of copper sulphate at one fifth the ferrous sulphate rate.
4. Two per cent. dormant spray of copper sulphate.

Experiment 3. On the same date as Experiment 2, fifteen small, stunted apple trees, *var.* Hereford Cross on M.I, II and XII rootstocks, which had shown zinc deficiency symptoms and summer die-back in previous seasons, were given the following treatments in triplicate :

1. Control—no copper sulphate.
2. 4 per cent. copper sulphate dormant spray.
3. 2 per cent. ,, ,, ,, ,,
4. ½ lb. ,, ,, per tree, soil application.
5. Trunk injection of solid copper sulphate.

All the trees were given a foliage spray of 0·1 per cent. zinc sulphate on 25th May, 1949.

Experiment 4.—On 7th March, 1950, three half standard apple trees, *var.* Crane's Seedling No. 304 on M.XII rootstock, which showed die-back and chlorosis in previous years, were injected with solid copper sulphate on a branch basis, using 0·15 gm. for each branch of approximately 2 in. in diameter. Four branches on each tree were injected. On 20th April, 1950, four branches per tree were sprayed with a 4:4:50 Bordeaux mixture. In addition one of the trees was given a foliage spray of 0·1 per cent. zinc sulphate at the pink-bud stage.

Experiment 5.—On 20th April, 1950, eight large bush apple trees, *var.* Cellini Pippin on M.XII rootstock, which had shown leaf symptoms and shoot die-back in previous years, were given the following treatments in duplicate :

1. Control—no copper sprays.
2. 0·1 per cent. copper sulphate foliage spray.
3. 0·05 per cent. ,, ,, ,, ,,
4. 4:4:50 Bordeaux ,, ,,

In the previous year these trees had been sprayed with a 0·2 per cent. zinc sulphate solution.

Experiment 6.—A group of half standard pear trees, *var.* Bristol Cross, on pear rootstock were treated in 1950. About two to three years previously they had been vigorous and healthy, but had later stopped growth. The bark became very rough and deeply fissured, large areas were shed, and the branches began to die-back. The trees were in very poor condition when the treatments were applied in 1950 and it was realized that, in some instances, bark damage was so advanced that recovery was unlikely. The treatments given in duplicate on a tree basis were :

1. Control—no zinc or copper.
2. 0·2 per cent. zinc sulphate foliage spray, applied 2nd May, 1950.
3. 0·1 per cent zinc sulphate ,, ,, ,, ,, ,, ,,
4. Bordeaux foliage spray ,, ,, ,, ,,
5. Injection of solid copper sulphate using 0·15 gm. per branch 7th March, 1950.
6. 0·1 per cent. zinc sulphate + Bordeaux spray.
7. 0·1 per cent. zinc sulphate + copper sulphate injection.

In addition to the above experiments certain proprietary copper compounds were compared with dilute copper sulphate solutions on pear, *var.* Beurré Bedford. The limited number of trees of each variety at Wisley made it impossible to replicate the treatments adequately for statistical treatment of the results.

Chemical investigations.

Leaf samples for analysis were taken from the mid-stem parts of leader growths, to avoid contamination from spray residues, since the sprays had been applied before these leaves were formed.

The leaves, after drying, were crushed by hand, digested in mixed nitric and perchloric acids and the copper determined colorimetrically by the method of Holmes (8). The addition of pure sodium sulphate prior to the extraction of copper diethyldithiocarbamate in carbon tetrachloride ensured that the copper complex was completely removed. Available copper in soil was determined chemically and by the *Aspergillus niger* method (12).

RESULTS.

Experiment 1.—The copper spray caused some localized damage and slight defoliation of the older leaves, but at the end of the season the shoots were healthy and vigorous. The untreated shoots lacked vigour and exhibited all the symptoms previously described. Solid injection had only a slight beneficial effect in 1948.

In the following season, 1949, there was only a slight residual effect from the foliage spray, but a very marked beneficial effect from the solid injection. Shoots on the control branches lacked vigour, defoliated from the tip and later died. Shoots on the injected branches were very vigorous and showed no sign of premature defoliation or tip die-back. In 1950 the copper-treated branches were the only ones to carry fruit. By 1951 all the control branches had died. Leaves sampled on 30th August, 1949, for chemical analyses, gave the following results :

Control = 2·2 μg. Cu per gm. dry matter.
Sprayed with 0·1 per cent. copper sulphate = 2·4 μg. Cu per gm. dry matter.
Injected with copper sulphate = 5·1 μg. Cu per gm. dry matter.

Experiment 2.—All the copper treatments were effective in controlling die-back. The results for leaves sampled on 30th August, 1949, and 5th September, 1950, are given in Table I. The mean copper content of treated plants was slightly greater than that of controls but all values were below those from trees growing on copper-sufficient soils. The values for 1950 were much lower than those for 1949. The zinc content was normal.

TABLE I.

Experiment 2. The effect of treatments on the mean copper content of leaves from the leader growth of apple var. *Crane's Seedling No. 856.*

Treatment, 1949	μg. per gm. dry matter (p.p.m.)		
	Cu August, 1949	Cu September, 1950	Zn September, 1950
Control. No copper	3·0	1·1	35·1
2% copper sulphate dormant spray . .	3·2	1·6	27·7
Soil application. ½ lb. copper sulphate per tree	4·0	1·6	38·9
Solid injection of copper sulphate at 1/5 ferrous sulphate rate	4·0	2·1	28·4

Experiment 3.—All the copper treatments were effective in controlling die-back in 1949. The combination of zinc and copper treatments produced very vigorous new growth in trees that had been stunted for a number of years. In 1950 one of the trees, treated with 2 per cent. copper sulphate dormant spray in 1949, showed traces of die-back, but all other copper-treated trees made healthy growth. The control trees showed signs of die-back varying from a trace to severe. Analytical data for leaves are shown in Table II. The copper values for treated trees are slightly higher than for controls in 1950, and generally higher in 1949 than in 1950, but all are below the value for trees on copper-sufficient soils. The zinc spray raised the zinc content of the leaves to a normal value.

TABLE II.

Experiment 3. Effect of treatments on the copper and zinc content of leaves of the leader growths of apple var. *Hereford Cross. Mean of 3 tree samples. All trees received a 0·1 per cent. zinc sulphate spray.*

Treatment, 1949	µg. per gm. dry matter (p.p.m.)		
	Cu August, 1949	Cu September, 1950	Zn September, 1950
Control. No copper	3·0	1·3	35·8
4% copper sulphate dormant spray	3·1	1·5	24·4
2% copper sulphate dormant spray . .	3·5	1·5	25·3
Soil application, ½ lb. copper sulphate per tree	2·8	2·0	16·8
Solid injection copper sulphate at 1/5 ferrous sulphate rate	2·4	1·7	30·9

Experiment 4.—Solid injection of copper sulphate produced vigorous healthy growth and the shoots were free from die-back. No damage was caused by the copper salt to branches or leaves. The copper sulphate was contained in gelatine capsules, which prevented contact of the salt with the bark at the time of injection.

The Bordeaux spray caused severe damage to the old leaves but the new growth was healthy.

Control branches lacked vigour, and die-back was medium to severe. The mean copper and zinc contents for the leaves are given in Table III. In 1951 the leaves and stems from the upper and lower portions of the leader shoots were analysed separately.

As in previous experiments, copper treatments stimulated growth and controlled deficiency symptoms without increasing the percentage copper content of the leaves and stems. The differences in copper content between upper and lower leaves and stems respectively were small. The zinc content of the upper half of the stems was approximately twice that of the lower half.

Experiment 5.—All copper treatments produced vigorous new growth and prevented die-back of shoots. Bordeaux sprays caused slight damage to the leaves, 0·1 per cent. copper sulphate trace to slight damage and 0·05 per cent. copper sulphate no damage. The effect of treatments on the copper content of leaves is shown in Table IV. Bordeaux and 0·1 per cent. copper sulphate sprays raised the copper content of leaves slightly above that of control trees. The zinc content of these trees was normal, showing the efficacy of a 0·2 per cent. zinc sulphate foliage spray in the previous year.

Table III.

Experiment 4. Effect of treatments on the copper and zinc content of leaves and stems of leader growth of apple var. *Crane's Seedling No. 304. Mean of three tree samples.*

Treatment, 1949	Leaf and stem position	μg. per gm. dry matter (p.p.m.)					
		September, 1950		September, 1951			
		Cu	Zn	Cu		Zn	
		Leaves	Leaves	Leaves	Stems	Leaves	Stems
Control. No copper	Upper	—	—	2·3	1·3	18·1	15·1
	Middle	2·2	16·8	—	—	—	—
	Lower	—	—	2·7	1·6	16·8	8·1
Solid injection 0·15 gm. copper sulphate per branch	Upper	—	—	2·4	1·6	15·2	14·1
	Middle	1·9	13·1	—	—	—	—
	Lower	—	—	2·6	2·0	14·9	6·1
Bordeaux spray (4:4:50) ..	Middle	1·9	13·3	—	—	—	—

Experiment 6.—Trees receiving zinc only gradually deteriorated and by the end of August, 1950, the leaves were mostly dead. Trees receiving copper, either as a foliage spray or by injection, were healthier although none made much extension growth. The Bordeaux spray caused medium to severe damage to the leaves. Copper-treated trees made better growth during 1951 but the recovery was not as good in pears as in apples. This was probably due to the more severe bark damage on the trunk previously mentioned. The mean copper content of the leaves from control trees on the 4th September, 1950, was 3·4 μg. and that of treated trees 5·2 μg. per gm. dry matter.

Table IV.

Experiment 5. The effect of foliage sprays of copper compounds on die-back and copper content of apple leaves, var. *Cellini Pippin on Malling No. XII rootstock.*

Treatment 20.4.50	Spray damage 2.5.50	Die-back	μg. per gm. dry matter (p.p.m.) September, 1950	
			Cu	Zn
Control. No copper ..	—	Slight-medium	1·8	32·4
0·05% copper sulphate ..	Nil	Nil	1·3	24·9
0·10% copper sulphate ..	Trace-slight	Nil	2·6	46·7
Bordeaux (4:4:50) ..	Slight	Nil	3·8	33·6

Spray damage.

Bordeaux mixture caused severe leaf damage and defoliation, particularly with pears. A number of proprietary copper compounds containing ammoniacal copper carbonate and copper oxychloride caused slight damage to apple and pear leaves when used at the dilutions recommended by the manufacturers for use as fungicides. Copper sulphate solution at 0·05 per cent., plus a wetting agent, caused no damage to apple or pear leaves when used from petal-fall onwards.

TABLE V.

Copper contents of normal and deficient leaves of fruit trees from various centres.

Fruit and location	Plant part analysed	Cu as μg. per gm. dry matter (p.p.m.)	Visual symptoms
Apple			
Laxton's Pearmain (Wisley)	Leaf	1·4–2·3	Shoot die-back
Hereford Cross ,,	,,	1·3–3·0	,, ,,
Gulval Seedling ,,	,,	1·2–1·9	,, ,,
Cellini Pippin ,,	,,	1·5	,, ,,
Lane's Prince Albert (Long Ashton)	,,	5·1–7·9	Normal
Edward VII ,, ,,	,,	6·5–9·0	,,
Laxton's Superb (Cannington, Somerset)	,,	5·6	,,
Worcester Pearmain (Cannington, Somerset)	,,	5·0	,,
Worcester Pearmain (Kingston Langley, Wilts.)	,,	2·3	Die-back
Worcester Pearmain (Berks.)	,,	13·6	Mg deficient
Pear			
Conference on Quince (Gloucester)	Leaf	8·0	Normal
Conference on Quince (Exeter)	,,	1·1	Die-back
Ornamental Crab			
Veitch's Scarlet (Exeter)	Top leaves Bottom leaves	2·2 2·5	" Little leaf " " Little leaf " Other fruits showed die-back at this centre
Cherry			
Sweet Cherry (Holland)	Leaf	14·2	" Rosetting "
Morello Cherry (Exeter)	,,	3·1	Die-back
Almond			
Variety unknown (Exeter)	,,	3·1	Die-back

Copper content of leaves and soils from Wisley and other centres.

The copper content of leaves from deficient and healthy plants is given in Table V. The threshold value for deficiency is about 5 μg. of copper per gm. leaf dry matter (p.p.m.). Table VI contains values for available copper from normal and deficient soils. The threshold level for copper in soils, by the *Aspergillus* method, is about 2 μg. per gm. air-dry soil. This is confirmed by the values for the fen soils which induce " withertip " symptoms in wheat.

TABLE VI.

The available copper content of soils as determined by Aspergillus niger (M).

Location	Depth of soil sample (in.)	Cu as μg. per gm. air-dry soil (p.p.m.)	Copper deficiency in crops
Wisley (Surrey)	0–6 6–12	0·8 0·4	*Apple and Pear* Severe summer dieback
Wisley (Surrey)	0–6 6–12	1·2 0·8	*Apple and Pear* Slight shoot dieback
Wisley (Surrey)	0–6 6–12	3–4 2	*Apple and Pear* Normal
Liss (Hants)	0–6 6–12	0·8 0·6	*Apple* Severe die-back
Methwold Fen (Norfolk) ..	0–6 6–12	1·0 0·8	*Wheat* " Withertip " symptoms
Ramsey (Huntingdon) ..	0–6 6–12	2·0 1·0	*Wheat* " Withertip " symptoms
Long Ashton (Somerset) ..	0–6 6–12	25 15	Nil

DISCUSSION.

Soil and plant analyses, together with responses to copper treatments, have shown that the summer die-back of shoots of fruit trees at Wisley and the other centres examined is caused by a deficiency of copper. The available copper content of soil in the affected areas at Wisley was less than the threshold value of 2 μg. per gm. air-dry soil as determined by the *Aspergillus niger* method. The leaves from affected shoots also contained less copper than did those from normal shoots, the threshold value being about 5 μg. per gm. leaf dry matter.

Oats, wheat and barley, grown on the site, showed "withertip" symptoms and the Cu status varied from 2 to 4 μg. per gm. dry matter. This provided confirmatory evidence of low copper status. Affected trees responded to copper whether it was applied to the soil as copper sulphate or to the trees by injections, dormant sprays or foliage sprays. The new growth on all treated apples was vigorous and free from necrotic spotting and die-back. Analyses of leaves from the new growths, however, did not show a substantial increase in the copper content. This phenomenon has been observed by Oserkowsky and Thomas (13) in pear. They found that normal and affected leaves, respectively, from trees affected with " exanthema " had the same copper content expressed as p.p.m. of dry matter. They suggested that affected leaves contained less active copper than did healthy ones in the same orchard. In contrast, leaves from trees affected with " exanthema " contained 3·2 to 5·1 p.p.m. of copper in dry matter, whereas healthy leaves from areas free from the disorder contained from 10-41 p.p.m. of copper.

Experiments carried out by Steenbjerg (17) with cereals may provide the reason for the small increases observed in the copper content of apple leaves treated with copper salts. He found that when cereals grown in copper-deficient soils were treated with increasing amounts of copper compounds, the stimulation of growth and dry matter production, at the lower levels, outweighed the increased copper absorption, with the result that the copper content, expressed as p.p.m. of dry matter, decreased. When he plotted dry matter produced against copper absorbed, he obtained an S-shaped curve with an initial trough. It is possible that in some instances our treatments stimulated growth to a greater extent than copper absorption with the result that the copper content, expressed as a percentage of dry matter, was not increased above that of the deficient shoots, although the total amount of copper within the treated shoots was greater.

All the copper treatments employed corrected the symptoms though some treatments caused more damage to the leaves than did others. Sprays at 4 per cent. concentration of copper sulphate applied during the dormant season were effective and caused no damage to the trees. Bordeaux sprays caused medium to severe damage, particularly to pear. Dilute solutions of copper sulphate (0·05 per cent.) plus a wetting agent were effective in controlling die-back, when applied before the death of the growing point of the shoot occurred, and they caused no foliage damage to apple or pear. The response to the treatments was very rapid (See Plate IV, Fig. 4.)

So far, copper deficiency in fruit trees has been diagnosed mainly on the light, sandy soils of Southern England and, with one exception, in an acid Greensand soil, has occurred in association with zinc deficiency.

SUMMARY.

1. Copper deficiency symptoms in apple and pear are described and illustrated.

2. The threshold copper level in apple and pear leaves, associated with the onset of visual symptoms, is <5 μg. per gm. dry matter (p.p.m.).

3. Soils providing adequate copper for fruit trees give values of >2 μg. of available copper per gm. of air-dry soil, as determined by the *Aspergillus niger* method.

4. Copper deficiency in fruit trees was corrected by applications of copper sulphate $CuSO_4.5H_2O$ as follows, (*a*) to the soil at the rate of ½ lb. per tree, (*b*) by 4 per cent. dormant sprays, (*c*) foliage sprays (0·05 per cent.) and (*d*) by branch or trunk injections.

5. Response to treatment was not always accompanied by an increase in the copper content of the leaves, expressed as a percentage of dry matter.

ACKNOWLEDGMENTS.

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PLATE 1

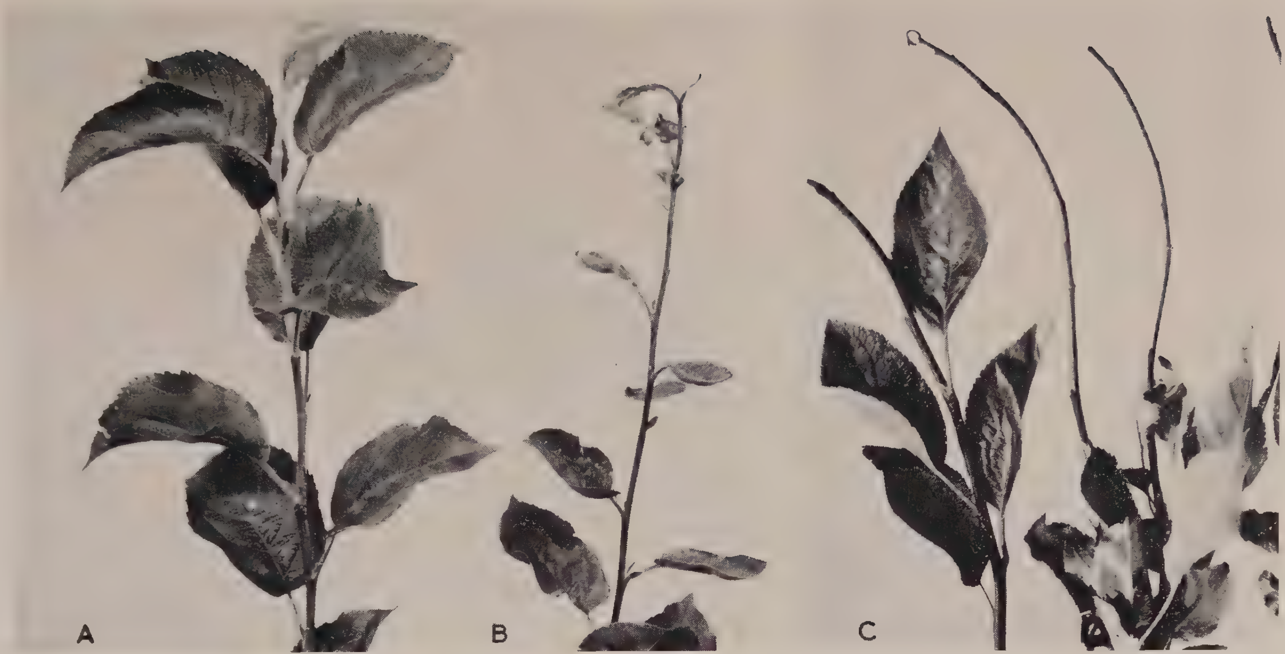
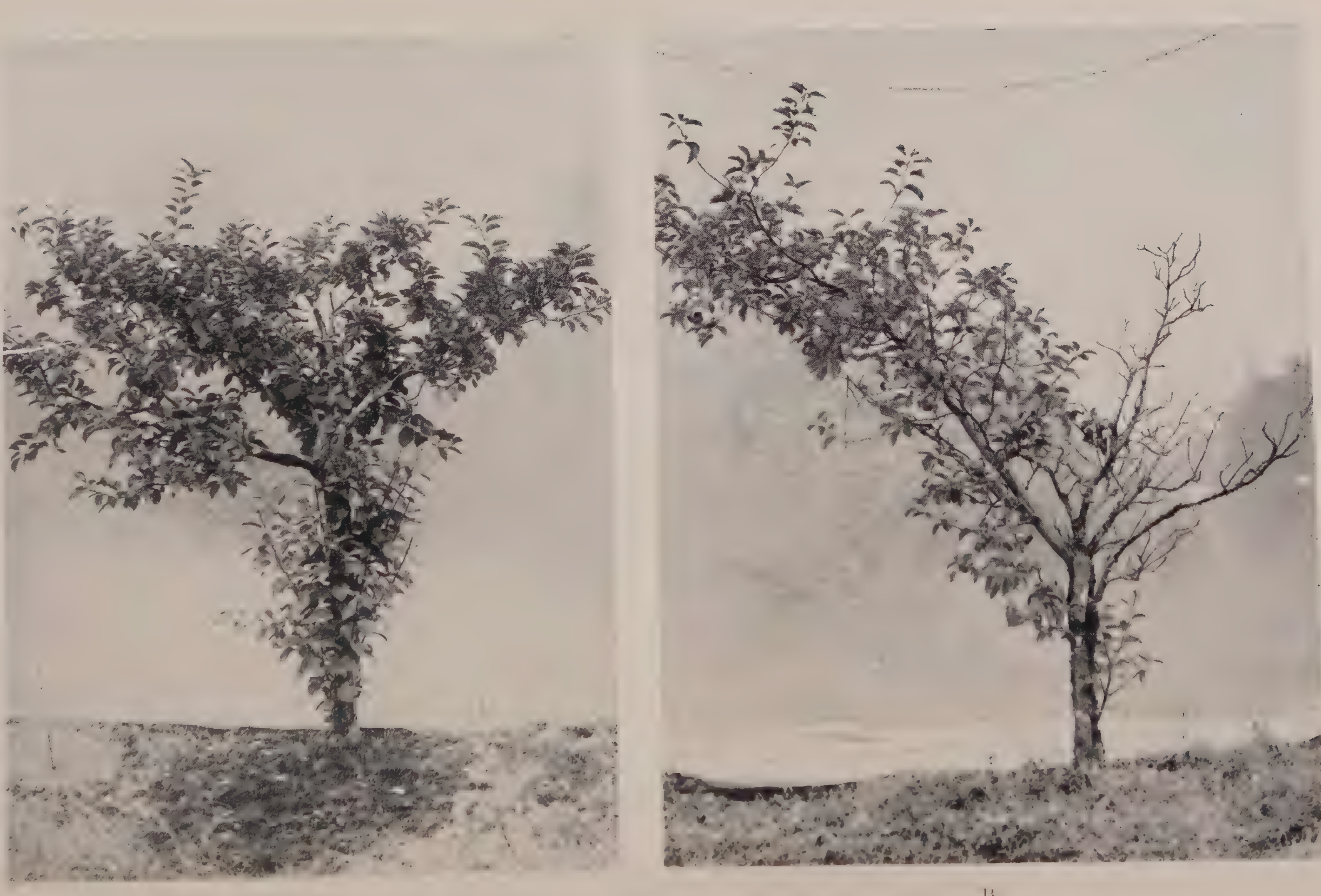


FIG. 1.

Copper deficiency in apple ; *var.* Gloucester Cross.

A. Normal.
B. Distortion of terminal leaves, upward cupping, and onset of defoliation.
C. Summer die-back of shoots (wither tip).

PLATE II


A.

B

Fig. 2.

Copper deficiency in apple ; *var.* Gloucester Cross on M.XII

PLATE III

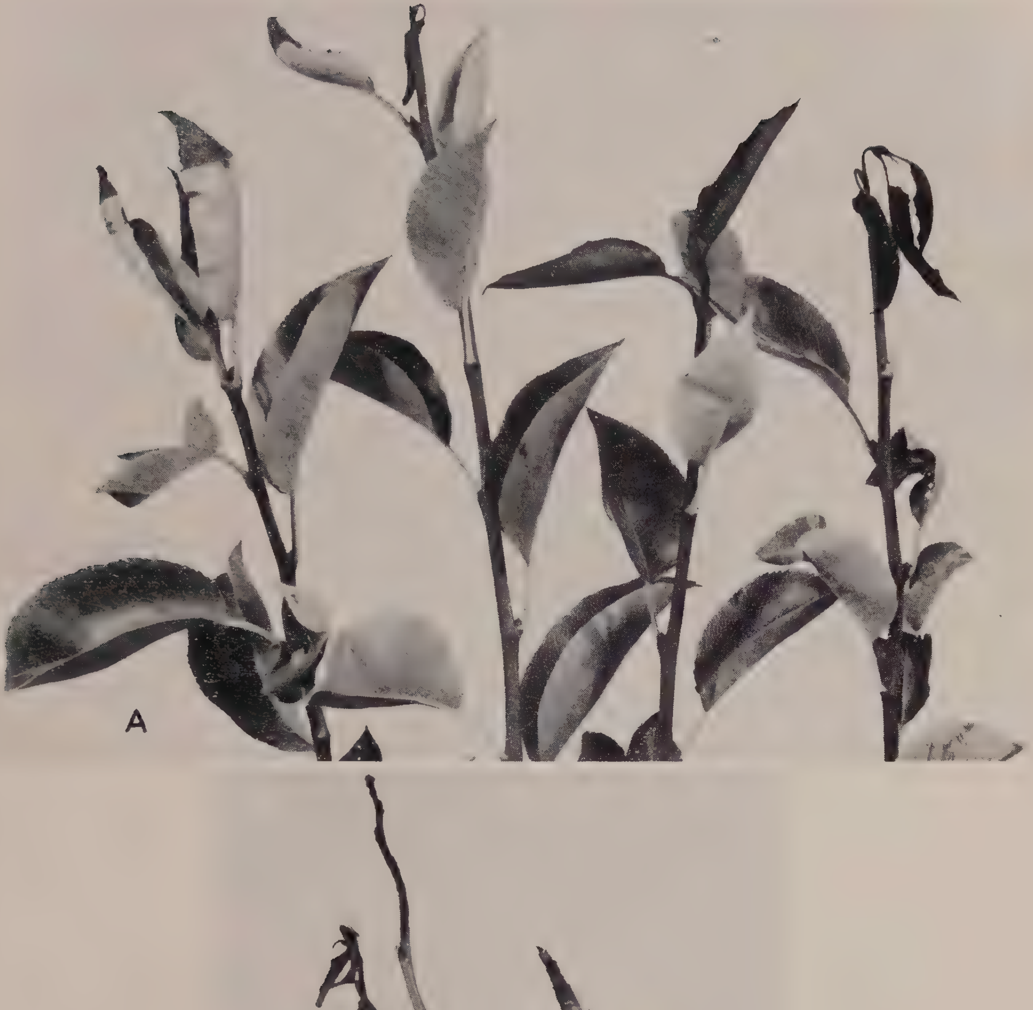


FIG. 3.
Copper deficiency in pear. A. Showing necrosis of terminal leaves. B. Showing shoot die-back.

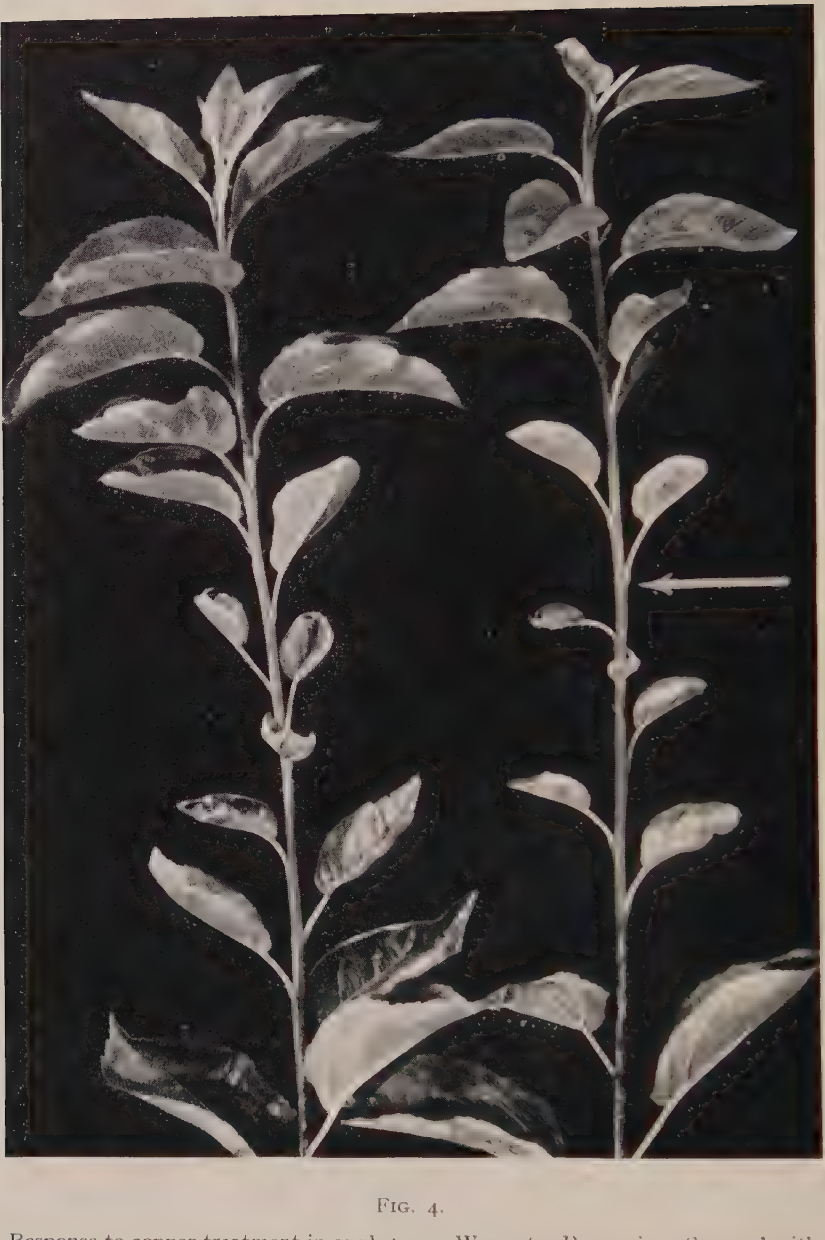


Fig. 4.

Response to copper treatment in apple; *var.* Worcester Pearmain. Sprayed with 0·05 per cent. copper sulphate solution 22nd June, 1950 at stage shown by arrow. Photographed 11th July, 1950.

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DIDYMELLA STEM ROT OF THE TOMATO

By P. H. WILLIAMS, ENID SHEARD and W. H. READ
Experimental and Research Station, Cheshunt

STEM Rot caused by *Didymella lycopersici* Kleb. has been known in Great Britain for many years. Massee described a disease resembling it, from Waltham Cross, Herts, in 1909 and called it Tomato Canker. He identified the causal organism as *Mycosphaerella citrullina* (C. O. Smith) Grossenb. and claimed that he had infected vegetable marrows with spores from tomato (Massee, 1915). Later Brooks and Searle (1921) reported that a fruit rot of tomato in this country was caused by *Diplodina lycopersici* Hollós, now known as *Didymella lycopersici* Kleb. They claimed that *M. citrullina* did not occur in Great Britain and considered that a number of herbarium specimens of *M. citrullina* on tomato stems were actually *D. lycopersici*. Recently *M. citrullina* has been found in this country on cucumbers and melons (Moore and Moore, 1949). Cross inoculations with *D. lycopersici* and *M. citrullina* by one of us (E.S.), have shown that their host ranges are distinct.

Didymella Stem Rot appears to have been abundant and destructive before and during the first World War, but after 1920 it was uncommon, only a few specimens being received at Cheshunt each year until 1942. In that year, serious outbreaks of the disease occurred and its severity, both in glasshouse and outdoor crops, increased until 1945. Since then it has declined but is still a serious menace to the tomato crop.

The investigations discussed in this paper, and hitherto described only briefly in the annual Reports of the Cheshunt Experimental Station, started in 1942 and have been concerned with the disease as it occurs in glasshouses.

SYMPTOMS.

Usually the disease is first noticed in glasshouses when isolated plants collapse suddenly during the early summer. Examination shows a dark brown, slightly sunken lesion girdling the stems at or near soil level (Fig. 1). The epidermis and cortex are rotted and the xylem is brown for some distance up the stem. The pycnidia of the fungus (Fig. 3), embedded in the rotten tissue, are usually the only fruiting stage, although Hickman (1944) has found perithecia on outdoor plants in this country.

Later in the season, similar but larger lesions appear higher up the stem, the pith often being destroyed (Fig. 2). Their position suggests that they have originated from infection through wounds where leaves or shoots have been removed. In some cases, these are the only lesions found, the so-called primary lesions at soil level being absent.

Considerable difficulty is experienced by growers in distinguishing these lesions from those caused by *Botrytis cinerea* Fr. and many past outbreaks of Didymella Stem Rot may have passed unnoticed for this reason. The lesions caused by *B. cinerea* are paler in colour and the cortex is hard. The characteristic grey mould is also usually present.

Fruit under glass is not usually attacked until late in the season, thus differing from the outdoor crop where fruit rot is very common and often the only symptom. The spores lodge under the calyx, causing an extensive black rot. The fruit may or may not fall off. In the latter case, the fungus may grow back into the pedicel and ultimately reach the stem.

Rotting of the hypocotyl region and the upper portions of the main roots also occurs. Hickman (1946) found this type of lesion was common in plants raised from contaminated seed and attributed it to infection from the seed during propagation. Very few of the specimens submitted for examination to us between 1942 and 1946 showed this type of lesion.

Lesions on leaves and sepals have also been seen occasionally by us on plants under glass where the disease was exceptionally severe.

HOST RANGE.

Successful inoculations of a number of plants, mainly members of the Solanaceae, with *D. lycopersici* have been reported.

Small (1928) ascribed a disease of the strawberry to *D. lycopersici* and made successful cross inoculations with cultures from strawberry and tomato. Van Poeteren (1928) also reported isolation of *D. lycopersici* from strawberry. Liesau (1932) states that several of the Solanaceae, including tomato and *Solanum nigrum*, were readily infected, lesions showing in thirteen days. In another group, the incubation period was much longer. It included *Datura stramonium*, tobacco, potato, egg plant and *S. dulcamara*. Klebahn (1921) was unable to infect any of the Cucurbitaceae except *Citrullus vulgaris* on which there were a few pycnidia bearing two-celled spores.

In our experiments, some possible hosts were tested by spraying wounded and unwounded stems with spore suspensions. Tomato plants were included as controls. Of the species tested, only the egg plant (*Solanum melongena*) proved readily susceptible to infection. Stem rot and, later, lesions on the leaves were produced and pycnidia were abundant on the lesions.

Wounded stems of *Solanum nigrum* became infected and the plants died. Unwounded plants remained healthy except when inoculated late in the year. In this they may parallel the tomato, older plants being more susceptible than younger.

Potato stems inoculated at the end of July remained healthy, but senescent stems inoculated in October became infected and died. Wounded stems were more susceptible than unwounded.

Slight infection was also obtained on wounded stems of *Nicotiana glutinosa* and *N. tabacum*. It was impossible to infect cucumber or melon, nor could Small's infection of strawberry be repeated.

From these experiments, *Solanum nigrum* seems to be the only alternative host on which *D. lycopersici* may overwinter. The hard woody stem may persist over the winter and if infected late in the year may form a source of spores in the spring. Potatoes near an infected tomato crop may become infected late in the season, but the ploughing in and rapid decay of the haulm should remove any risk of infection being carried over to the next year unless tomatoes are grown on the same ground.

The other plants which we have successfully inoculated are too rarely grown to be of any importance as alternative hosts.

SOURCES OF INFECTION.

A number of possible sources of infection have been suggested. Of these, the principal are the soil and airborne spores derived from rubbish heaps containing diseased stems and fruit. Infected or contaminated seeds, canes and strings used for supporting the plants may play a lesser part.

(A). SOIL.

Infected soil is probably the source of many of the primary infections at the base of the stem, but it has not been possible to determine whether it or the airborne spore is more important. A number of experiments have been made to determine the conditions that favour the spread and persistence of *D. lycopersici* in the soil and comparisons have been made between growth in sterilized and in unsterilized soil.

In the work with soil, described below, a standard compost consisting of 4 parts of maiden loam to 1 of stable manure was prepared. It was air-dried, sifted through a 3 mm. sieve and stored in the laboratory. When required for use, a sample was adjusted to the required water content, apportioned to a series of flasks and sterilized for 30 minutes at 15 lb. pressure. The inoculum was a pure culture spore suspension obtained in the following way.

Cultures were grown either on tomato stems sterilized with propylene oxide (Snyder and Hansen, 1947) or on slopes of Hawker's Medium A (Hawker, 1939) to which tomato juice from stems and leaves, sterilized by filtration, had been added aseptically. On both media, the fungus produced numerous pycnidia and a spore suspension was readily obtained by flooding with sterile distilled water.

The growth of *D. lycopersici* was estimated by plating 25 g. samples. Various dilutions were employed at first but, later, two sets of plates were poured from each sample, one at 1 in 10,000 and one at 1 in 100,000. From these it was possible to choose one that gave counts of from 30 to 50 colonies per plate. Ten plates were poured at each dilution. The medium used was Czapek-Dox agar to which 0·008 per cent. rose bengal had been added. This medium was found to be the most satisfactory in suppressing bacterial competition in plates poured from unsterilized soil and was adopted for all studies for the sake of uniformity. The plates were incubated for three weeks on the laboratory bench since exposure to light favours the production of carbonized hyphae and aids in the quick recognition and counting of colonies. Counts are shown in the Tables as numbers per milligram of oven-dry soil.

Volume of soil.

Two soils were used, the standard compost and a potting compost consisting of 3 parts of maiden loam to 1 of old cucumber bed. Two series of flasks were prepared from each, one of 300 g. of soil in 500 ml. flasks and the other of 90 g. in 250 ml. flasks. The water content was adjusted to 50 per cent. saturation. The 300 g. series received 3 ml. of spore suspension per flask and the 90 g. series 1 ml.

In both soils the number of colonies of *D. lycopersici* was much higher in the 90 g. series (Table I). Since the ratio of soil surface to soil volume was greater in these flasks than in the 300 g. series, it was concluded that the growth of the fungus was mainly in the surface layers of the soil, a fact of some importance when considering the question of soil disinfection in glasshouses.

TABLE I.

Volume of soil and growth of D. lycopersici. *Numbers of colonies per mg. of dry compost.*

Weeks	Loam + old cucumber bed		Loam + stable manure	
	300 g.	90 g.	300 g.	90 g.
4	285	1,037	1,436	11,100
6	867	6,613	1,635	12,570
8	797	1,625	3,262	13,340
12	554	4,408	3,248	12,140

Organic matter.

In the experiment described above, considerably more growth was obtained in the flasks containing soil plus stable manure than in the corresponding ones containing soil plus old cucumber bed (Table I). In the latter material, the stable manure was completely decomposed. It seemed possible that the increased growth might be due to undecomposed cellulose in the stable manure. In two further experiments, therefore, partly decomposed stable manure and fresh wheat straw were added to the loam-cucumber bed mixture. To facilitate mixing, both were air-dried and then pulverized in a hammer mill. They were added to the compost at 1 per cent., 5 per cent., and 10 per cent. by weight and the moisture capacity of each mixture determined. One hundred gram lots in 250 ml. flasks at 50 per cent. saturation were inoculated with 1 ml. of spore suspension.

Both materials greatly increased the growth of *D. lycopersici*, straw being much more active than stable manure. (Tables II and III.) These results suggest that stable manure containing a high proportion of undecomposed straw, either dug into the soil or as a mulch, may favour the growth of *D. lycopersici*. Orth (1939) states that stem rot was more severe on plots receiving fresh stable manure.

TABLE II.

Stable manure and growth of D. lycopersici. *Numbers of colonies per mg. of medium.*

Weeks	Percentage (by weight) stable manure in the medium			
	0%	1%	5%	10%
3	6,834	7,246	15,138	18,855
5	8,675	5,498	15,694	23,263
7	4,747	3,627	12,324	15,305
9	9,934	6,203	13,979	23,430
11	7,401	10,708	18,596	25,440

Water content.

Soil cultures (300 g.) were set up at 15, 30, 50, 75, and 100 per cent. saturation. They were incubated on the laboratory bench and samples plated 3, 5, 7 and 26 weeks after inoculation.

TABLE III.

Wheat straw and growth of D. lycopersici. *Numbers of colonies per mg. of medium.*

Weeks	Percentage (by weight) wheat straw in the medium			
	0%	1%	5%	10%
3	3,819	12,000	36,070	52,820
5	7,311	17,840	33,930	56,460
7	7,644	21,350	46,310	69,720
9	6,316	17,580	28,540	61,630
11	6,732	17,580	46,060	65,700

Table IV shows that the fungus grows over a wide range of water content, the optimum being 50-75 per cent. saturation. The comparatively little growth at 100 per cent. saturation is rather surprising in view of later results when the water content was increased to saturation after incubation. The growth of the fungus at 15 per cent. saturation, an almost air-dry condition, is also interesting.

TABLE IV.

Influence of water content on growth of D. lycopersici. *Numbers of colonies per mg. of medium.*

Weeks	Water content (per cent. of saturation)				
	100	75	50	30	15
3	14	241	307	376	0
5	68	800	2,314	225	0
7	218	1,624	1,565	510	0
26	67	452	590	177	4

Temperature and water content.

During our experiments we found that the fungus had completely disappeared from the soil of a glasshouse where a high degree of infection had occurred the previous summer. Between the two tomato crops, the house had been used for propagating cucumbers. The temperature had been maintained at 65° F. to 70° F. for about 9 weeks and the soil had been rather wet as a result of watering and syringing the young plants. It seemed possible that the disappearance of *D. lycopersici* was due to the high temperature and/or soil moisture.

Soil cultures (water content 50 per cent. saturation) were incubated on the bench for five weeks and then the amount of *D. lycopersici* in six flasks was determined. The water content of half the flasks was then raised to 100 per cent. by the addition of sterile distilled water. Equal numbers of " normal " and " wet " flasks were placed at 27°, 17° and 4° C. At four-weekly intervals one flask was withdrawn from each series and samples plated. (Table V.)

TABLE V.

Temperature and soil moisture and growth of D. lycopersici. *Numbers of colonies per mg. of dry soil.*

Weeks	27° C.		17° C.		4° C.	
	Saturation of medium		Saturation of medium		Saturation of medium	
	100%	50%	100%	50%	100%	50%
4	41	17	10,775	9,797	18,006	9,679
8	111	16	10,786	5,941	13,080	6,732
12	66	2	10,943	6,801	18,838	7,900
16	112	3	878	11,051	16,524	9,377

The numbers in the flasks kept at 27° C. show a striking fall from the number at the beginning of treatment, 9,720 per mg. of dry soil. The addition of water counteracted the adverse effect of high temperature to some extent, possibly by preventing desiccation. At 4° C. it produced a considerable increase in growth. This result suggests that reinfection of steamed soil during the winter may be favoured by prevailing low temperatures and high moisture content of the soil, which is always heavily flooded with water after steaming.

In other experiments, *D. lycopersici* grown in soil at 50 per cent. saturation survived for 20 weeks at 27° C., but was killed in flasks at 30° C.

Growth and survival in steamed and unsteamed soil.

The disease is frequently very severe in crops on steamed soil ; in fact, after " steaming ", it has often made its first appearance on a nursery. It may be expected that if sterilized soil becomes reinfected by airborne spores or other means, the fungus will spread through the soil with greater rapidity owing to diminished competition. Another factor which may influence the severity of the disease is the more luxuriant growth of the plants in steamed soil. Shoots produced in the lowest leaf axils are larger than those on unsteamed soil and the wounds made in removing them correspondingly larger, while the more luxuriant foliage tends to keep the base of the stem moister and prevents wounds, made in removing shoots and lower leaves, from drying up rapidly. It is known that these conditions definitely favour the occurrence of basal stem rot, caused by *Botrytis cinerea*, which is rare except on plants growing in steamed soil.

To investigate this, a small glasshouse was divided into six plots of which four were steam sterilized. As soon as the soil had cooled, all the plots were watered with a spore suspension derived from infected stems. The sterilized plots were planted with tomatoes, variety Potentate, 3 days, 2, 4 and 10 weeks, respectively, after inoculation and the unsterilized plots after 3 days and 10 weeks, respectively. Plants were removed when they wilted and the presence of *D. lycopersici* confirmed.

All the plants on the sterilized plots, planted 3 days, 2 and 4 weeks after inoculation, had become infected 12 weeks after planting. The experiment ended 9 weeks after planting the fourth plot by which time 44 per cent. had become infected. Of the unsterilized plots, that planted 3 days after inoculation showed 44 per cent.

infection after 12 weeks and that planted 10 weeks after inoculation, none. There is, therefore, some direct evidence that steam sterilization favours infection by *D. lycopersici.*

Investigation of the relative growth in steamed and unsteamed soil is made difficult by the problem of eliminating other members of the soil microflora without affecting the growth of *D. lycopersici.* Two methods have been used: (1) the use of a differential medium for plating and (2) the use of tomato plants as indicators.

(1) *Soil plating experiments.* After a number of preliminary experiments, it was found that the addition of 0·008 per cent. rose bengal to Dox agar eliminated the worst types of spreading bacteria. Since all other organisms are not completely eliminated by this method, the results are only tentative because competition between organisms in the plates may reduce the number of colonies of *D. lycopersici.*

Where spores were used as inoculum, soil cultures were prepared in the usual manner, the water content being 50 per cent. saturation. Before inoculation, half the flasks were partially sterilized by placing them in an autoclave, with the water boiling, and taking pressure up to 10 lb. The gas was then turned out and the flasks removed as soon as the pressure had fallen. The whole procedure took 20 minutes.

The unsterilized flasks proved to be heavily contaminated with *Penicillium* sp., and no *Didymella* appeared on the plates. No antibiotic factor seemed to be involved, for zones of inhibition did not appear when the fungi were grown together in the same plate. In the steamed soil, *D. lycopersici* survived for 45 weeks.

Where cultures were used as inoculum, a quantity of compost was steamed for 30 minutes in a small apparatus in the laboratory. When cool, a sufficient quantity (5,600 g.) was placed in a glass tank. An equal quantity of unsteamed soil was placed in another tank and sufficient water added to equalize the water contents of both soils. Two days later, 970 g. of a sand-oatmeal culture of *D. lycopersici* was thoroughly mixed with each. Samples were plated, twice weekly, for 16 weeks.

The data are too numerous to present in full but it may be stated that, up to 11 weeks after inoculation, the number of colonies of *D. lycopersici* from the steamed soil was 2 to 3 times that of colonies from the unsteamed. The later occurrence of the fungus became sporadic and no consistent difference could be detected.

(2) *Plants used as indicators.* Twenty 10-in. pots were filled with compost ; the contents of ten were steamed in the laboratory and the soil was returned to the pots. One hundred grams of sand-oatmeal culture were then mixed with the contents of each pot. They were covered with brown paper and were stored in the laboratory, water loss being made up periodically.

After 8 weeks incubation, one pot from each series was removed and the contents well mixed. Each compost was then applied as a one inch surface layer to the soil of ten tomato plants in 6 in. pots. The plants were examined 5 weeks later. This process was repeated every 4 weeks until the supply of compost was exhausted. The last pots were tested 44 weeks after inoculation of the soil.

The proportion of plants that became infected was small, but there is some indication that the fungus was more abundant in the steamed soil (Table VI). Of more importance is the fact that it persisted for so long in both soils.

While these experiments are few in number, it is noteworthy that greater success in demonstrating the presence and survival of the fungus in unsterilized soil has been

TABLE VI.

Growth and survival of D. lycopersici *in steamed and unsteamed soil.*

Number of weeks after inoculation of the soil	Number of plants infected out of 10	
	Soil of inoculum steamed	Soil of inoculum unsteamed
8	2	0
12	1	2
16	2	1
20	1	2
24	3	0
28	6	1
32	3	2
36	5	1
44	1	1
Total	24	10

attained where cultures have been used as an inoculum. Cultures may be regarded as the equivalent of diseased plant remains since mycelium is present in both. It may, therefore, be suggested that where diseased plant remains are left in unsterilized soil the fungus is likely to remain in the soil for a considerable period. Where, however, such soil is exposed to infection by airborne spores, the chances of the fungus establishing itself are much reduced. On the other hand, steam sterilized soil may be readily infected by spores and the fungus, having made a certain amount of growth, may persist for some time.

(B). SPORES.

Air-borne spores form a second important source of infection. They have been detected by exposing petri dishes containing Dox agar for one minute both in glasshouses and outside on infected nurseries. Colonies resembling *D. lycopersici* were transferred to agar slopes and tested for pathogenicity. By this means, spores were found in the glasshouses containing infected plants in spring and early summer, and outdoors throughout the year. Considering the comparative inefficiency of the method, it is evident that large numbers of spores must be present in the atmosphere. The trapping of spores outdoors during January and February, when the houses were empty, suggests that they may come from diseased plants on rubbish heaps. Examination of such a heap revealed infected haulms bearing pycnidia containing viable spores.

Spores show a considerable resistance to desiccation. Drops of spore suspension were dried on slides and stored in the dark at laboratory temperature. Each day a number of these deposits were tested for viability by wetting with dilute tomato juice and incubating in a moist chamber. As the spores germinated after 15 days exposure to dryness, it seems possible that they can be carried a considerable distance by air currents before losing their viability.

Spores, whether in suspension or in the pycnidia, have proved very resistant to low temperatures.

Small glass tubes containing 7 ml. of a spore suspension were placed in the freezing compartment of a refrigerator at about −5° C. Each day one of the tubes was removed and, after thawing, the spores were centrifuged out and transferred to dilute tomato juice. Drops of this suspension were put to germinate at 20° C. Viability gradually decreased, falling to 20 per cent. in 24 hours after 6 weeks, although the majority germinated in 48 hours. By the end of 9 weeks, viability had fallen to almost nil, only 2 per cent. germinating in 72 hours.

Spores in pycnidia appear even more resistant to cold. Pieces of infected stem were placed in the freezing compartment. Each day a small piece of tissue bearing pycnidia was removed and placed in a glass cell containing water. Drops of the resultant spore suspension were pipetted on to slides and there mixed with tomato juice. Germination was still 100 per cent. after 12 weeks when the supply of pycnidia was exhausted.

Airborne spores may be responsible for two types of infection, (a) reinfection of sterilized soil leading to an outbreak of primary basal lesions and (b) secondary infections higher up the stems, where splashing of infected soil during watering is not likely to occur. Many outbreaks, when a few scattered plants become infected on nurseries where no disease had occurred the year before, may also be due to airborne infection.

Undoubtedly also, the rapid spread of the disease and occurrence of lesions on stems up to a height of 18 in. is due to the distribution of spores washed from lesions when watering.

(c). SEEDS.

Seeds taken from diseased fruit are commonly black in colour and bear pycnidia of the fungus. It is also possible that mycelium may be present in bits of pulp adhering to imperfectly washed seed, but it is unlikely that free spores adhering to the seed coat would survive long enough to act as sources of infection.

Several workers consider that infected seed is an important source of infection (Van Poeteren, 1928 ; Bremer, 1933). Ogilvie (1945) obtained 8·5 per cent. and 5 per cent. of infected seedlings, respectively, from two lots of seed. Hickman (1946) reports that 34 per cent. of plants raised from infected seed became diseased when planted on land which had never carried a tomato crop. In the same experiment, 25 per cent. of plants raised from healthy seed, with which 2 per cent. of diseased seed had been mixed, became diseased. Unfortunately no plants raised from healthy seed appear to have been grown, so that the possibility of the disease having originated from some source other than the seed was not excluded.

Other authors (Orth, 1939 ; Small, 1939) consider that infected seed rarely gives rise to infected plants.

In our experiments, germination of infected seed was poor (50 per cent.). No seedlings were infected although some emerged bearing the infected seed coats on the tips of the cotyledons and no plants from these seedlings became diseased during three months growth. Most of the seed used in the tomato industry is taken from glasshouse crops early in the season when fruit rot is very uncommon. Seed cannot, therefore, be regarded as a very important source of infection, but very careful selection of fruit for seed is advisable, when seed is saved from outdoor plants, owing to the prevalence of fruit rot on such crops.

(D). OTHER SOURCES.

Several investigators have suggested that canes and other supports may harbour the fungus (Kordes, 1933 ; Small, 1937 ; Hickman, 1946), and our observations support this view.

Unsterilized wire supports were obtained in the spring from a nursery where the disease had been severe the previous year. The mixture of soil and rust at the bottom end was scraped off, applied to wounded tomato stems and covered with moist cotton wool. Several infections resulted. Similarly, string used to support infected plants, was shown to harbour the fungus.

D. lycopersici grew and fruited on straw and grew slightly on wood, raffia and cardboard taken from a " sink pot " as used in the cultivation of tomatoes, when these materials had been sterilized with propylene oxide. The fungus also grew on a number of other materials such as hay, rotten wood and leaf mould when they had been autoclaved, but may not be able to colonize them when unsterilized. Of the materials tested, only straw appears likely to be of importance but no evidence has been obtained as yet that it favours the spread of *Didymella* when used as a mulch.

EFFECT OF CULTURAL CONDITIONS.

TEMPERATURE AND HUMIDITY.

In pure culture, the optimum temperature for growth of *D. lycopersici* is about 20° C. It appears to be comparatively sensitive to high temperatures, since we have found that growth on Dox agar plates falls off from 1·3 cm. *per diem* at 20° C. to 0·6 cm. at 25° C. At 30° C. no growth occurred but the fungus was not killed after a week's exposure. In the soil, the fungus shows a similar sensitivity.

These investigations suggest that the fungus is more active at lower temperatures. It has been stated that the disease is worse during cool, wet weather (Heinsen, 1921, Liesau, 1932) and our observations agree with this. Lack of temperature-controlled glasshouses has prevented experiments on this question.

MANURIAL TREATMENT.

In experiments with the variety Potentate in 6 in. pots, no significant differences in susceptibility to attack were observed when nitrogen, potash and phosphate were varied over a wide range. Similar results were obtained with the varieties Potentate and Ailsa Craig growing in 10 in. pots. It has not been possible to carry out large-scale experiments with plants growing in the borders.

CONTROL.

Various recommendations have been made in the past for controlling Didymella Stem Rot, such as the use of Bordeaux Mixture (Heinsen, 1921) and Uspulun or other mercurials (Hahmann, 1929 ; Bremer, 1933 ; Kordes, 1934 ; Koch, 1934). The use of clean seed, treatment of canes and destruction of diseased haulms have also been recognized as important (Kordes, 1934 ; Small, 1936 ; Orth, 1939). Our own experiments have been mainly devoted to finding substances to be watered on the soil or applied to wounds to prevent infection or used for the treatment of lesions to arrest their development. In the following account, however, other aspects of the problem are discussed.

DESTRUCTION OF DISEASED PLANTS.

The importance of diseased tomato haulms as a source of spores throughout the year has been emphasized above. This material should be destroyed but, in practice, its destruction is difficult since at the end of the season the amount of stems and roots may be about 40 tons per acre.

Burning sulphur at the rate of 1 lb. per 1,000 cubic feet has proved effective in drying up the plants and killing spores outside the pycnidia. Spores still within the pycnidia are unaffected. Unfortunately, this treatment cannot always be used because in calm weather the danger of sulphur dioxide in comparatively high concentration drifting to neighbouring dwelling houses or crops is considerable.

Burying diseased haulm or covering heaps with a layer of soil may be effective where the amount is small but is not practicable on large nurseries. Sometimes the haulm is carted from the nursery, but this only removes the centre of infection.

CULTURAL PRACTICES.

Observations on the growth of *D. lycopersici* in soil and on the effect of manurial treatments detailed in previous sections, do not offer much hope of controlling the disease by cultural means.

Stable manure and composted straw, which appear to stimulate the growth of the fungus in soil, are necessary for cultivation. Straw mulches may favour the disease by providing a medium on which the fungus may grow and by keeping the base of the stem moist, but observations made on the Cheshunt Experimental Station nursery during 1951 gave no evidence that straw mulches in affected houses caused any spread of the disease.

Steaming, which undoubtedly favours the disease, is a necessity on many nurseries, especially where the variety Potentate is grown. Possibly soil sterilization with 2 per cent. formalin (= 0·8 per cent. formaldehyde) may sometimes be usefully substituted for steaming, since it does not promote the same chemical changes in the soil as does steam sterilization.

Removing leaves and shoots only on bright sunny days, when the wounds will dry quickly, may help to prevent secondary infections. Watering the plants early in the day to prevent excessive humidity at night and plentiful ventilation may also be beneficial. With both these measures, however, the amount of labour available on the nursery is the overriding factor.

SOIL TREATMENT.

Where the fungus may be present in the soil at the end of the season, some form of soil sterilization is necessary. In laboratory experiments it was found that heating infected soil for 10 minutes at 50° C. killed the fungus. The normal steaming process in which the soil is raised to 100° C. and kept at that temperature for 10 minutes should, therefore, give an ample margin of safety. As pointed out above, however, the disease is often more severe after steaming and steamed soil appears to be more readily infected by airborne spores than is unsteamed. Accordingly, a number of substances have been tested for their ability to free the surface layers of the soil from such airborne infection.

In preliminary experiments, formalin (38 per cent. formaldehyde), a tar acid sterilizing fluid (41 per cent. phenols), mercuric chloride and malachite green were tested.

The soil of a glasshouse was steamed and 3 days later inoculated by watering, as evenly as possible, with a spore suspension. The house was then divided into 20 plots and 11 treatments were applied to the soil. Some plants were " watered in" with a pint of the solution in addition to or in lieu of the normal treatment of 1 gallon per sq. yd. All the plots were planted the day following treatment, except those treated with formaldehyde and the tar acid fluid, where planting was delayed for 12 days to avoid phytotoxic effects. Eighteen tomatoes, variety Potentate, were planted in each plot. The total number of infected plants in each plot when the experiment was ended, 10 weeks after planting, is shown in Table VII.

TABLE VII.

Soil treatments for the control of D. lycopersici. *Number of infected plants out of 18.*

Treatment	Plot 1	Plot 2	Mean
Control	18	13	15·5
Formalin 2% ; 1 gal. per sq. yd.	0	0	0
Tar acid fluid 2% ; 1 gal. per sq. yd.	0	0	0
$HgCl_2$ 0·05% ; 1 gal. per sq. yd. + 1 pint per plant	3	–	3
$HgCl_2$ 0·05% ; 1 gal. per sq. yd.	10	14	12
$HgCl_2$ 0·05% ; 1 pint per plant	14	15	14·5
$HgCl_2$ 0·05% ; 1 pint per plant twice	11	–	11
$HgCl_2$ 0·025% ; 2 gal. per sq. yd.	11	–	11
Malachite green 0·065% ; 1 gal. per sq. yd.	5	5	5
Malachite green 0·065% ; 1 pint per plant	3	8	5·5
Malachite green 0·05% and $HgCl_2$ 0·025% ; 1 gal. per sq. yd. ..	9	–	9

Both formaldehyde and the tar acid sterilizing fluid destroyed the fungus in the soil. Mercuric chloride applied when planting, in addition to previous treatment, and malachite green before planting, also gave a large reduction in infection.

Of these treatments, formalin 2 per cent. (= formaldehyde 0·8 per cent.) and the tar acid fluid at 1 per cent. were applied at the rate of 1 gallon per sq. yd. on commercial nurseries 14 to 21 days before planting. The treatments, however, failed to prevent losses from attacks at the base of the stem.

Following these experiments, a number of other substances were tested for toxicity to the spores of *D. lycopersici*. Spore suspensions were prepared by soaking in distilled water stems bearing lesions and filtering off any debris present through two layers of cheesecloth. For each test, 2 ml. of the suspension were pipetted into centrifuge tubes and the spores centrifuged out. After draining, 2 ml. of the appropriate solution were run into the tubes. Three methods of treatment were used.

(*a*) Drops of the spore suspension in the fungicidal fluid were placed on slides in petri dishes lined with moist filter paper.

(*b*) The solution was allowed to act for one hour. The spores were then centrifuged out and, after draining, were shaken up in dilute tomato juice and put to germinate as in (*a*).

(*c*) A duplicate tube was treated as in (*b*) except that the spores were washed twice with 10 ml. of distilled water to remove the test liquid before they were put on slides.

Of the substances tested, certain mercury compounds and dyes were the most effective. Since these substances are absorbed by the soil, some indication was sought of the strength necessary to kill spores in the soil. Accordingly, the solutions were shaken with an equal weight of soil for one hour, filtered and tested (Table VIII). The best of these substances was ethyl mercury phosphate.

TABLE VIII.

Toxicity of certain compounds to D. lycopersici *before and after shaking with soil. Least percentage concentrations inhibiting spore germination.*

Compound	Before shaking			After shaking		
	In solution	Treated 1 hour		In solution	Treated 1 hour	
		Drained	Washed		Drained	Washed
Mercuric chloride	0·01	0·01	0·01	0·13	0·2	0·2
Basic phenyl mercury nitrate	0·0005	0·0005	0·0005	0·03	0·02	0·04
Basic phenyl mercury borate	0·0002	0·0005	0·001	0·04	0·02	0·04
Ethyl mercury phosphate	0·00014	0·00014	0·0005	0·005	0·005	0·005
Malachite green	0·02	0·02	0·02	>0·2	>0·2	>0·2
Methic green	0·02	0·02	0·02	>0·1	>0·1	>0·1
Brilliant green	0·02	0·02	0·02	>0·1	>0·1	>0·1
Crystal violet	0·01	0·01	0·02	>0·1	>0·2	>0·2

The length of time for which a soil surface treated with ethyl mercury phosphate remained toxic to spores of *D. lycopersici* was then determined. Soil from a tomato border was steamed and placed in wooden boxes, the surface well pressed down and solutions of the compound applied through a fine rose so as to wet the top inch of soil. The boxes were covered with cellophane and the soil kept damp by spraying with tap water. Small glass cylinders were pressed into the soil and small quantities of spore suspension pipetted on to the soil inside the cylinders. After 24 hours, portions of the surface soil from inside the cylinders were removed and placed on slopes of Dox agar. Each week a fresh set of cylinders was placed on fresh areas of the soil. By this means, it was found that soil treated with 0·02 per cent. ethyl mercury phosphate remained toxic for 7 weeks and with 0·01 per cent. for 3 weeks. Control boxes, treated with water only, invariably yielded cultures of *Didymella*.

In the meantime, tests on young plants had shown that 0·01 per cent. ethyl mercury phosphate was toxic to them but that at 0·006 per cent. it caused only slight stunting. Tests showed that, at the latter strength, soil treated at the rate of 1 quart per sq. yd. remained toxic to *D. lycopersici* for 8 days and at 1 gallon per sq. yd. for 15 days.

In a small field trial, ethyl mercury phosphate at 0·006 per cent. gave a considerable degree of control. The soil of a small greenhouse was steamed and divided into 8 plots. Three days after steaming, each plot was watered with 2 gallons of a spore suspension. Pairs of plots were planted 3 days and 2, 4 and 10 weeks after inoculation, one plot of each pair having been treated two days previously with 0·006 per cent. ethyl mercury phosphate at the rate of 1 gallon per sq. yd. Diseased plants were removed as soon as seen and the presence of the fungus confirmed. In Table IX, the final percentages of diseased plants, 12 weeks after planting, are shown, except for the plots planted 10 weeks after inoculation. For these plots, circumstances necessitated taking the final readings 9 weeks after planting.

TABLE IX.

Soil treatment with ethyl mercury phosphate.

Time of planting after inoculation	Per cent. of diseased plants	
	Treated	Control
3 days	22	100
2 weeks ..	22	100
4 weeks ..	11	100
10 weeks ..	0	44

Subsequent trials on commercial nurseries have confirmed that treatment of steamed soil with 0·006 per cent. ethyl mercury phosphate at the rate of 1 gallon per sq. yd. gives a fair measure of protection against reinfection of the soil by *D. lycopersici*.

After the disease has appeared, the use of the same solution at the rate of ½ gallon per sq. yd. has been of value in preventing the spread of the disease. Where the diseased plants are few, it is only necessary to remove them and treat the surrounding soil but, where many plants are involved, it is necessary to treat the whole house.

In view of the poisonous nature and the vesicant action of the solid and of concentrated solutions of ethyl mercury phosphate, certain precautions must be observed. By one manufacturer, to obviate weighing on the nursery, it is supplied in small bottles containing enough for 40 gallons of spray. A dye has been incorporated so that if any is splashed on the skin, it may be instantly seen and washed off. Operators must wear rubber gloves and other protective clothing. The solution is applied with a can when the areas to be treated are small and with a spraying machine fitted with a fine rose in place of a nozzle where whole houses are to be treated. It has been found inadvisable to apply it to a straw mulch since amounts of vapour, dangerous to health and detrimental to the setting of the flowers, are evolved.

TREATMENT OF LESIONS.

Small (1936) suggests that small lesions may be cut out and the wound covered with a Bordeaux paste. Cultures from infected stems have, however, shown that from a lesion 1 cm. long, affecting only one side of the stem, the fungus may extend at least 15 cm. up the interior. With larger lesions at the base of the stem, it has been detected 40 cm. above the upper edge of the lesion. It is hardly surprising, therefore, that in our experiments the fungus has invariably grown out again even when all visibly infected tissue has been removed.

It has also been claimed that painting with creosote was effective in killing the fungus. In our trials, however, the fungus invariably grew out again beyond the treated area. Even if effective, such treatment would probably be too laborious for commercial application.

In other trials, stems at soil level were sprayed with a spore suspension after lightly wounding. When the lesions became visible, they were sprayed with a number of fungicides using approximately 50 ml. per stem so that the surrounding soil was also wetted. The substances and the maximum strengths at which they were applied were : mercuric chloride 0·5 per cent., lime-sulphur 10 per cent., copper sulphate 0·5 per cent., malachite green 0·25 per cent., potassium permanganate 1 per cent., copper naphthenate-petroleum emulsion (0·1 per cent. copper naphthenate, 2·75 per cent. petroleum) and Bordeaux mixture 5 per cent.

None of these treatments arrested the development of the disease. Healthy tomato plants were killed by the copper naphthenate-petroleum emulsion and damaged by 0·5 per cent. mercuric chloride and 1 per cent. potassium permanganate.

PREVENTION OF STEM INFECTIONS.

Many experiments have been made to test the value of fungicides in preventing the infection of stems of tomatoes by spores of *Didymella*, particularly infections *via* wounds made in the normal removal of leaves and side shoots.

The first trials were made in an endeavour to find a substance which would protect the collars of the plants and, since established plants are not readily injured by fungicides at these sites, concentrations highly phytotoxic to the foliage could be used. The test was conducted by spraying the bottoms of the stems of pot plants with the fungicides and, 24 hours later, applying a thin layer of soil containing 10 per cent. of a sand-oatmeal culture of *Didymella* round the collars of the plants.

Of the substances tested, only a proprietary salicylanilide preparation diluted to contain 0·5 per cent. salicylanilide had any appreciable action in reducing the number of infected plants.

Substances found ineffective at the stated concentrations were mercuric chloride 0·2 per cent., copper sulphate 0·5 per cent., lime-sulphur 10 per cent., malachite green 0·25 per cent., cuprous oxide suspension 1 per cent., cresylic acid 1 per cent., proprietary tar acid fluid (41 per cent. phenols) 0·25 per cent.

In another trial, the proprietary salicylanilide product was compared with thiram, which had given promising results in *in vitro* laboratory tests. The lower leaves of pot plants were cut off and the wounds on one series of plants sprayed 2 hours and, on another series, 24 hours after wounding, The fungicidal sprays employed were 0·5 per cent. salicylanilide and 0·5 per cent. thiram and the control plants were sprayed with water. The plants were inoculated by spraying with a spore suspension 24 hours after the fungicide application.

The results showed that a significant reduction in infection was obtained with 0·5 per cent. salicylanilide only. Further work has shown that the concentrations of salicylanilide required to give protection to wounds cause excessive deposits on fruit accidentally sprayed and are, in practice, uneconomic.

In view of the toxicity to spores shown by mercury compounds in *in vitro* tests, a number of organo-mercury compounds were tried as wound protectants in replicated trials in a glasshouse. The compounds tried at concentrations equivalent to 0·01 per cent. Hg and 0·0025 per cent. Hg were phenyl mercuric acetate and the phenyl-, n-propyl-, n-butyl-, n-amyl- and *n*-cetyl-mercuric chlorides. Two proprietary

PLATE I

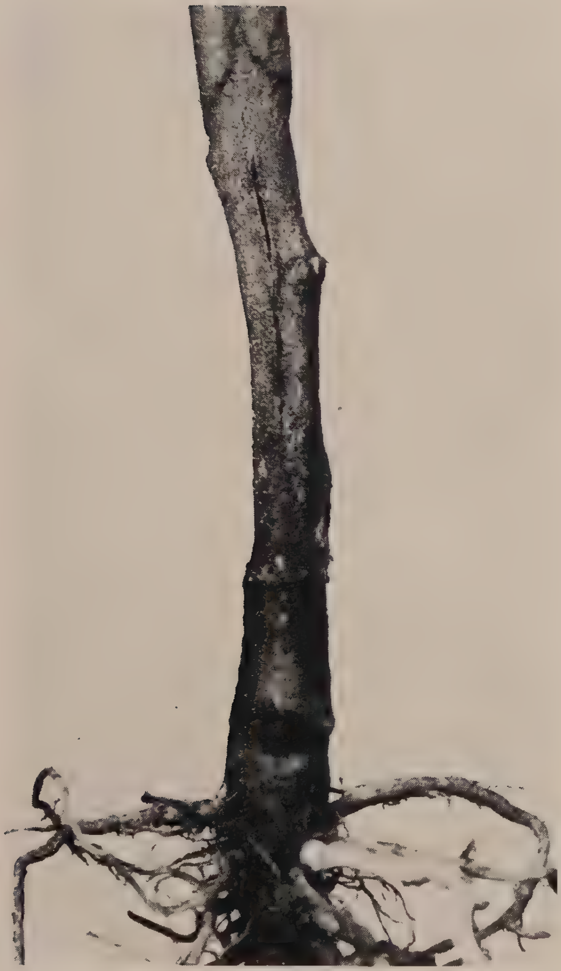

Fig. 1.

Basal lesion caused by *Didymella lycopersici* Kleb. on stem of tomato (× 1).

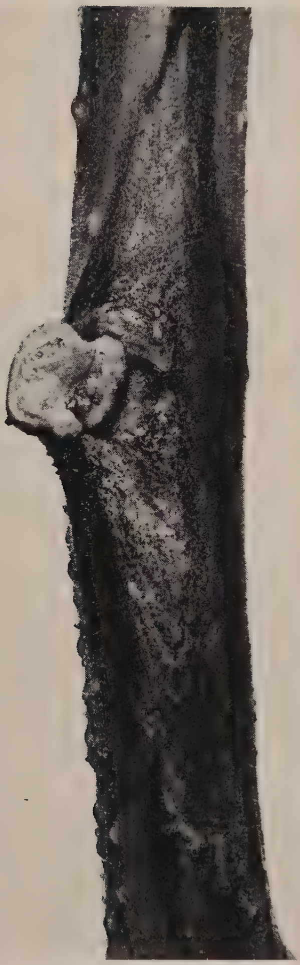

Fig. 2.

Lesion caused by *Didymella lycopersici* Kleb. on stem of tomato (× 2).

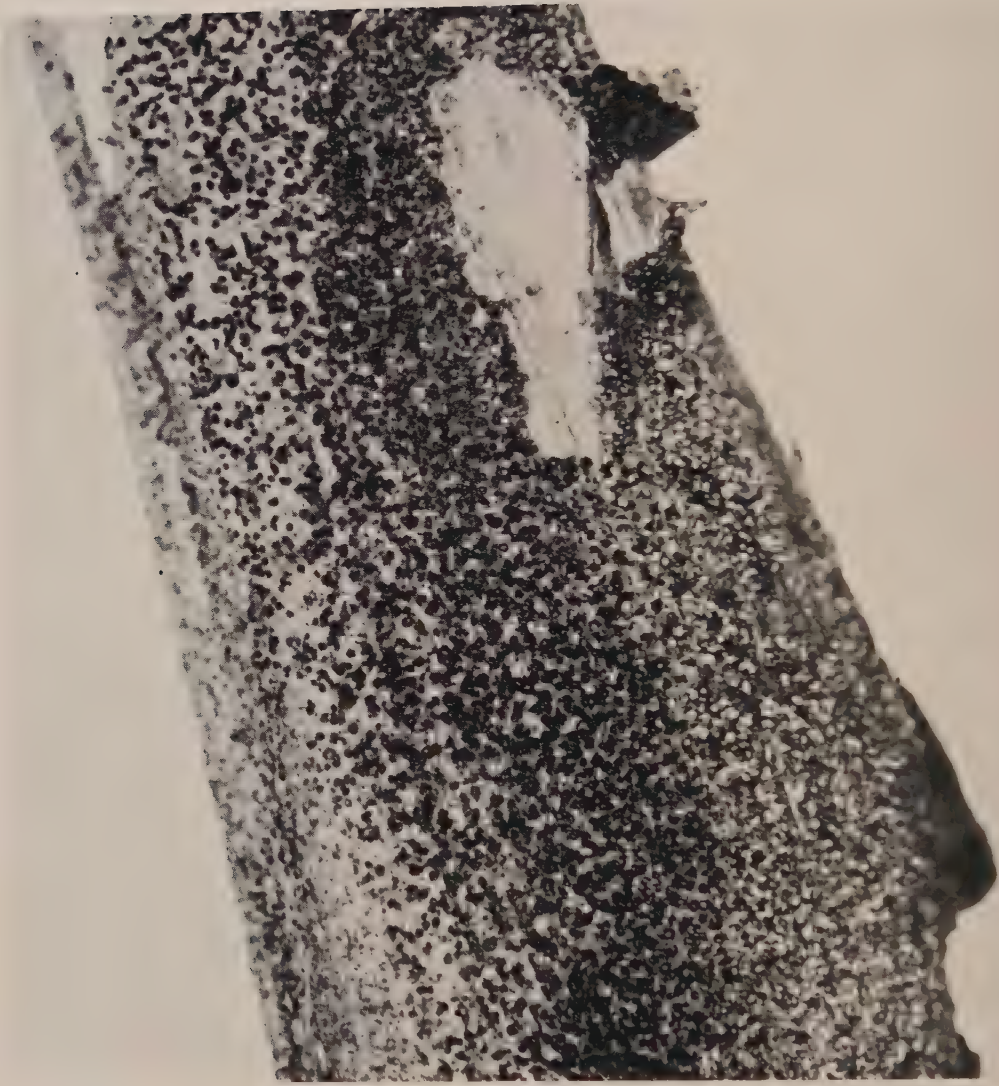

FIG. 3

Pycnidia of *Didymella lycopersici* Kleb. on stem of tomato (× 9).

products containing 2 per cent. and 1·5 per cent. phenyl mercuric chloride respectively, were also tried at dilutions equivalent to 0·01 per cent. and 0·0025 per cent. Hg.

None of these compounds, applied 4 hours after wounding, reduced the degree of infection resulting from inoculation 24 hours later. Neither did they reduce infection when applied 24 hours after inoculating wounds which had been made 4 hours previously.

Other trials were made with a product stated to contain polyethylene polysulphides and described by Stewart and Standen (1946). This product was stated to form an adherent, elastic film on sprayed surfaces. Sprays containing 0·6 per cent. and 0·3 per cent. of this product failed to prevent infection of wounds when applied either 24 hours before or 24 hours after inoculation.

SUMMARY.

1. The symptoms of Didymella Stem Rot, caused by *Didymella lycopersici* Kleb., are described. They include lesions on stem, hypocotyl, fruit and leaves. Only those on stems and fruit are common.

2. Of possible host plants, other than tomato, only *Solanum nigrum* appears likely to be of importance in harbouring the fungus.

3. The fungus grows in soil over a wide range of moisture content. Growth is favoured by the incorporation of stable manure and straw and by low temperatures and high water content, but is greatly curtailed by temperatures of 27° C. or over.

4. *D. lycopersici* infects soil sterilized by steam more readily than unsterilized soil but, when introduced as mycelium, can persist for at least 44 weeks in unsterilized soil.

5. Airborne spores have been trapped outside the glasshouses on infested nurseries throughout the year and form an important source for the re-infection of sterilized soil and for spreading the disease once it is established. The spores are very resistant to desiccation and low temperatures.

Other sources of infection such as seed, canes and string are of minor importance.

6. No evidence was obtained that varying the nitrogen, potash or phosphate content of the soil affected the susceptibility to infection.

7. Control measures are discussed. All diseased stems and fruit should be destroyed. Burning sulphur at the end of the season helps to dry up the plants, but is not always practicable. Control by cultural methods is not likely to prove successful. Cutting out and spraying lesions have not controlled the disease. A method of treating the soil with ethyl mercury phosphate, either to prevent reinfection of sterilized soil or to prevent spread of the disease in the growing crop, is described.

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REVIEWS

INTERNATIONAL COMMISSION FOR PLANT RAW MATERIAL. MATERIAE VEGETABILES. Vol. I, No. 1. (Holland: Dr. W. Junk, The Hague. 1952. Pp. 128, illus. Price Fl. 40 per volume.)

This new journal from Switzerland (Editors) and Holland (Publishers) is the organ of the International Commission for Plant Raw Materials set up as the result of the International Botanical Congress at Stockholm in 1950.

It is " dedicated ", we are told in the introduction, " to the whole domain of vegetable raw materials, . . . a connecting link on the one hand between research, cultivation and extraction, amelioration, preparation and utilization on the other." In fact the editor should not be short of papers which, it is proposed, will appear in " grammatically correct English, French, German, Italian or Spanish."

The first number contains two or three articles of horticultural or nearly horticultural interest, e.g. on the utilization of fibres from the stems of edible bananas, and on the Casuarinas as tanning materials.

The journal will appear four times a year.

May one indolent Englishman without a paper knife, ungrammatically but "right now", put in a plea that the leaves shall be cut before issue on each occasion ? Otherwise, for paper, appearance, diagrams, etc., full marks !

D.A.

PLANT ENVIRONMENT AND THE GROWER. By SIDNEY A. SEARLE. (London: C. F. Casella & Co. Ltd., W.1, and A. Gallenkamp & Co. Ltd., E.C.2. 1952. Pp. 50, illus. Price 5s.)

The author of this booklet is a horticultural consultant and the publishers are two well-known suppliers of scientific instruments. The contents are concerned with the need for, and the application of instruments to assist the grower of glasshouse crops, chiefly tomatoes, in the establishment and control of a satisfactory plant climate and of suitable soil moisture and temperature conditions.

The information given is supported by quite a wide selection of abstracts of, and quotations from recent scientific publications, well over half of which are American. A useful section on soil moisture tensiometers and their application is included.

J.E.G.

THE FRUIT YEAR BOOK, 1953. The Royal Horticultural Society. (London. October, 1952. Pp. 137, illus. Price 15s.)

October has always been a rather particular month for connoisseurs of fruit and, this year, with the Doyenné du Comice pears and the first Cox's Orange Pippins, the fruit lover will welcome the Sixth Fruit Year Book. If he cannot afford a decanter of port with which to enjoy his dessert, he can, we hope, at least look forward to a comfortable chair in front of the first log fire of winter, in which to study the experiences of growers of fruit at home and in many different parts of the world. This volume is dedicated to Mr. Tom Neame, who grows fruit not only as a business but because it gives him pleasure to do so, and who himself contributes an account of his 40,000 mile journey to three continents to visit the fruitgrowing areas of the world. It may be comforting to us at home to know that, at the end of it all, he and his son thought how fortunate they were to be fruitgrowers in England.

The *Fruit Year Book* is primarily intended for the amateur and many of the articles in this volume are written specially for him. There are also contributions that describe different aspects of commercial fruitgrowing, particularly abroad ; but the amateur will find much of interest to him in these also.

Space does not permit the detailed mention of each of the papers contained in this volume. Besides the account of Mr. Neame's journey, there are descriptions of fruitgrowing in Spain, Jamaica and South America. Mr. Norbury writes a fascinating story of the influence of the West Midlands on fruitgrowing ; it is as well for those who grow fruit in other parts of the country to be reminded of the great contributions to horticultural research, literature and varieties that emanate from Gloucestershire, Herefordshire, Warwickshire and Worcestershire, where fruit has been grown since very early times. There are several articles on the training and pruning of fruit trees, and those members of the Fruit Group who visited Foots Cray Place some years ago will be particularly interested in the process of training a winged pyramid apple in the garden at Bradbourne, East Malling. Few amateurs can afford vineries in these days ; grape enthusiasts will, therefore, read with all the more pleasure the two articles on varieties that can be grown outdoors. Some of us who have visited North America in the late summer have yearned to grow blueberries at home ; it is encouraging to learn that those who garden on an acid soil well supplied with moisture may find them worthy of trial. However, they must keep the birds and rabbits off them, and in this connection they will find Lt. Gen. Wason's notes on protection against birds worth study.

We wish the R.H.S. Fruit Group continuing prosperity and look forward to future volumes of its Annual.

T.N.H.

POPLARS. By T. R. PEARCE. (Forestry Commission Bulletin No. 19. London : H.M. Stationery Office, Kingsway. 1952. Pp. 50, illus. Price 7s. 6d.)

Those interested in poplars and desirous of trying a timber crop widely grown on the Continent, but to only a small extent in the U.K., will find much of interest and value in the Forestry Commission's Bulletin No. 19 by T. R. Pearce, M.A. Although extensively grown as screens or even as specimen trees on account of their rapid growth, few people have as yet grown poplars on a commercial scale in Britain. There is, however, a steady demand for this useful timber for veneer and plywood, matches, pulp for paper and wood-wool. Its resistance to splintering makes it useful for certain purposes, while it is eminently suitable for box-making, as it is odourless and resin-free.

The Bulletin lists the four main sections of the genus *Populus*, viz. : White Poplars, Aspens, Balsam Poplars and Black Poplars, the familiar Lombardy Poplar " *P. Nigra* var. Italica du Roi " occurring in the last section. It then gives botanical descriptions of the commoner species and hybrids, their respective nursery and silvicultural requirements and their resistance to disease.

Emphasis is laid particularly on the susceptibility or otherwise of each variety to rust and bacterial canker, which seem to be the two most important diseases.

The Bulletin points out that much hybridizing has taken place. Many of these hybrids have not been observed for a long enough period to determine their resistance to disease or their form and rate of growth and, therefore, at present, the Forestry Commission is limiting its distribution of cuttings to four varieties only. In view of the risk of importing undesirable varieties, poplars may be imported only under licence and in very small quantities, unless the source is known.

Mr. Pearce then goes on to discuss the culture of poplars, the type of soil needed and the water requirements, which appear to be fairly high. He suggests that the poplar can profitably be planted in odd corners or margins of land. Road side planting is satisfactory except on clay soils, where they may cause shrinkage of the clay and damage to road foundations. For the same reason, they should not be planted near buildings. Acid soils should be avoided.

Propagation, planting and pruning are dealt with in detail and tables are included, showing the growth rates of several varieties under different conditions.

Details are given of the fairly numerous insect pests which attack the poplar, as well as of the various fungal and bacterial troubles.

Finally the properties and uses of poplar timber are described in some detail, and a useful bibliography is to be found at the end.

The Bulletin is embellished with a number of excellent reproductions of photographs showing not only the growing tree at all stages, but also the insect pests which attack it.

T.N.

THE FUNDAMENTALS OF FRUIT PRODUCTION. By V. R. GARDNER, F. C. BRADFORD and H. D. HOOKER, Jr. New Third Edition. (McGraw Hill Publications in the Agricultural Sciences. 1952. Pp. 739, illus. Price 76s. 6d. $9.00.)

When the first edition of *The Fundamentals of Fruit Production* appeared in 1922, it largely achieved its aim of drawing together in an easily accessible form the widely scattered results of pomological and related research. Revisions for the second edition were few and piece-meal and it was to be hoped that the third edition, which has just appeared, would show considerable modification in the light of the advances in knowledge over the past thirty years. This has been achieved to some extent by two completely new sections that have been added to deal with the important subjects of light relations and growth regulators, but it seems unfortunate that it has been necessary to omit the sections on vegetative propagation and geographical influences to accommodate them. Apart from the new sections, revision has, however, been very incomplete. One cannot help wondering that so many of the fundamentals were firmly established before the beginning of the twentieth century, judging by the tabulated data and the bibliographies. Pomological research subsequent to 1940 receives scant notice. The use of terms such as " recent " and " growing belief that " are definitely misleading as they cover some publications dated more than thirty years ago. The impact of virus diseases escapes mention and most of the modern work by Crane and others on pollen compatibility is omitted. Reference to English work on soil management is limited to the work of Bedford and Pickering published in 1919. The very considerable volume of modern research on the diagnosis of nutritional deficiencies is inadequately covered, while the work of East Malling on rootstocks is passed over by a misquoted reference (p. 516) to incompatibility of Conference on quince rootstocks.

The general production is up to the usual high standard of McGraw Hill, but the index could with advantage be more complete and it would be easier to locate the references if the sectional bibliographies were all combined in a list at the end instead of being distributed through the book. The third edition occupies 49 pages less than the second edition.

While it is probably true that this book now requires extensive rewriting, it is still in a class of its own as a text book of pomological principles ; research workers and fruitgrowers as well as students will doubtless refer to it for guidance as frequently as those of the previous generation referred to the original edition.

H.B.S.M.

REGISTER OF NEW FRUIT AND NUT VARIETIES 1920-1950. By R. M. Brooks and H. P. Olmo. (U.S.A. : University of California Press, Berkeley and Los Angeles. 1952. Pp. 206. Price 22s. 6d.)

In almost all parts of North America the breeding and testing of new varieties of fruits occupies an important place in the research programme. Since 1944, a series of papers by Brooks and Olmo, of Davis Campus, University of California, in the Proceedings of the American Society for Horticultural Science, have provided descriptions of the more important fruit and nut varieties originating in North America during the past thirty years. The information in these papers has now been collected in one volume, with indexes under species, name, place of origin and patent number. Without such valuable reference books, it is no easy matter to keep informed about the many new introductions or even to know their places of origin, from which reliable information may be obtained.

Descriptions are given of 1,055 varieties of fruit and 51 of nuts ; the information in each case includes origin, date of commercial introduction, patent number and trademark name, parentage and chief characters of fruit and plant. The different kinds of fruit are grouped together but it would be useful if, in future editions, each page were headed with the group name to avoid turning many pages to find the heading in the text—no light task as there are some 20 pages of apples and 35 pages of peaches.

Few of the varieties described have been tried in Great Britain but several have shown some promise, e.g. Cortland apple, Bauer Thornless loganberry, Red Lake currant, Gorham pear and Newburgh raspberry. The list purports to cover only North American varieties but John Innes and Merton Thornless blackberries are described ; further it is stated that ornamental species that do not produce edible fruit are excluded, yet the third entry in the book, the Almond-Peach Maniton, is described as such. It is unexpected also to find varieties of Tung included.

This book should be of special value to plant-breeders and may stimulate someone to produce a similar description of varieties originating in Great Britain.

H.B.S.M.

PLANT DISEASES IN ORCHARD AND GARDEN CROPS. By Ernst Gram and Anna Weber. Edited and adapted for English conditions by R. W. G. Dennis. (London : Macdonald & Co. (Publishers), Ltd. 1952. Pp. 618, illus. Price 90s.)

This book is impressive in size and content. Its authors are two well-known

Danish practising plant pathologists who have behind them a wealth of many years' advisory contacts with all branches of the horticultural industry in that country. It was first undertaken in 1933, but, owing to the outbreak of the second world war, its publication in Denmark was delayed until 1940. The second Danish edition of 1944 is the basis of the present English version, and the editing and free adaptation of the original for this purpose has been ably done by Dr. R. W. G. Dennis of the Royal Botanic Gardens, Kew, himself a well-known botanist and plant pathologist. Evelyn Ramsden is the translator.

The book is not designed as a reference manual for plant pathologists, but as a practical handbook for horticultural growers and advisers, and from this standpoint its large " family bible " size and weight are disadvantageous. The heavy glossy art-paper on which the work is produced might well have been sacrificed in favour of a handier, and portable, format.

The whole field of plant diseases, parasitic and non-parasitic, is covered in five main sections. The first one, " The Nature of Plant Diseases " provides a lucid prefatory survey of all the pathogenic causes comprehended by the diseases to be dealt with individually in the next three sections. In these the description of each disease and its control is given, under its common name, and these are grouped in alphabetical order under the common names of the host plants, also arranged alphabetically. The host plants are further grouped as tree and bush fruit (II), vegetables and herbaceous fruit (III), and ornamental plants and trees (IV). The concluding section (V) deals with the general subject of control measures under the sub-headings of (1) administrative action, (2) action by the grower, and (3) chemical fungicides.

It is refreshing to meet a text book of economic plant diseases thus planned primarily from the standpoint of the host plants and their cultivators, and it is, therefore, all the more disappointing to have to record two major handicaps to its achievement of maximum usefulness. Firstly, in view of the fact that the control of plant disease is only one of the many aspects of successful horticultural practice upon which the grower needs handbooks, the price of this book—£4 10s.—is likely to prove prohibitive for the majority of potential users. Secondly, the value of this book as a work of handy references for the non-pathologist would have been greatly enhanced if more attention had been given to aids to diagnosis by the provision of more extensive and elaborate keys to disease identification. Accounts of individual diseases are useless to the grower if, in a particular instance, he does not know which one to read. The summaries given at the ends of the sections on each host could have been placed at the beginning, and elaborated, with great advantage.

The knowledge of crop diseases and their control has greatly advanced since the 1944 Danish edition was produced, but the Editor of this English version has gone a long way towards filling this gap. Even so there are many omissions and not a few mis-statements of fact which the appropriate specialist on each disease or host will doubtless identify for himself. Here it would be invidious to quote particular instances where elaboration or correction are needed. The value of the book is enhanced by a wealth of drawings in monochrome and colour, and of photographs. In the preparation of the English edition 32 of the original monochrome illustrations were replaced by 27 new ones from English sources. The colour plates are those of the Danish edition, and the standard of colour veracity in these is so poor that one feels that potential purchasers could profitably have been spared the heavy cost of their inclusion. A comprehensive bibliography of literature is added to each section, and the work concludes with an index to the scientific names of the pathogens, and to those common names of plant diseases which are distinctive.

R.V.H.

FIELD EXPERIMENTATION WITH FRUIT TREES AND OTHER PERENNIAL PLANTS. Technical Communication No. 23, Commonwealth Bureau of Horticulture and Plantation Crops. By S. C. PEARCE. (Farnham Royal: Commonwealth Agricultural Bureaux. 1953. Pp. 131, illus. Price 10s.)

Since Fisher in 1925 started to apply his elegant statistical methods to the theory and practice of field experimentation, their use has extended all over the world and to every conceivable crop. Books, pamphlets and papers have appeared in profusion for the guidance of experimentalists in the use of these methods, which have reached a high degree of elaboration, almost entirely with the requirements of annual crops in view.

The impact of the new methods on experimentation with perennial crops was immediate. By 1930 they were being applied to a range of fruit crops and to tea and rubber with success, but, as years went on, with an increasing realization that long term perennials presented many problems and many opportunities not encountered in annual arable crops. There has long been a need for a publication specifically devoted to perennials, and workers in this field will welcome the monograph under review from so experienced a hand as that of Dr. S. C. Pearce of the East Malling Research Station.

Dr. Pearce's publication is comprehensive without being superficial: there are nine chapters and four statistical appendices and an excellent bibliography and index. After a useful introduction that makes clear what statistics can and, equally important, cannot do, three chapters are devoted to the principles of design. These are followed by two sections on details of design embracing the problems of plot size, shape, replication and the precautions needed in varying types of trial ranging through manurial, cultivation, variety and plant protection experiments; precautions without which otherwise well designed experiments may prove unsatisfactory. There are chapters on the analysis of results and the devices to be adopted when mishaps and incomplete data, which are serious hazards on long term perennial experiments, have to be dealt with. The monograph ends with a chapter on ancillary measurements which is specially valuable for its treatment of sampling and technical errors.

The author has been at particular pains to choose his language and illustrative matter and, whilst the essay is not easy reading it is straightforward reading. In some places rather more expansion would have been welcome, as for example in dealing with the pros and cons of factorial experiments.

Different readers will find different aspects of particular help and interest. In a review one can only mention a few personal to the reviewer. The sections on the interpretation of significance should clarify a good deal of confused thinking on this subject. Dr. Pearce modestly refrains from pressing his own view-point exclusively. The tendency of this reviewer would be towards a somewhat stricter attitude than Dr. Pearce adopts. He would, for instance, ponder dubiously upon an interaction between indistinguishable main effects. He has, in fact, been caught out at the game. But on the question of nomination as a check on "digging out" something significant he is wholeheartedly with the author. How salutary is Dr. Pearce's warning against producing mathematical relationships, as out of a hat, without being able in a straightforward English sentence to say what they mean in terms of the experiment and of horticulture.

Other sections of note are those on the modification of experiments that have outrun their original usefulness and on the treatment of several years' results. Expansion here would have been justified.

Only one production error has been noted for correction in future reprints. In Appendix II, page 102, there is a footnote on notation. It would never have occurred to the reviewer that $(a + b \times c)$ could mean $(a + b)c$. The use of the full-stop notation to clarify this point is fraught with danger to the beginner as may be seen on lines 13 and 16 where what is meant to be a full-stop is printed as a decimal point.

This monograph has obviously been a labour of love to its author : the engaging quotations at the beginnings of the chapters are one, but not the only indication of this. It should be studied section by section by all engaged in experimental work on perennial crops for it is full of wise advice.

T.E.

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